Agnes M. Claypole

Jan. 1897

BIOLOGICAL LECTURES

DELIVERED AT

THE MARINE BIOLOGICAL LABORATORY

OF WOOD'S HOLL

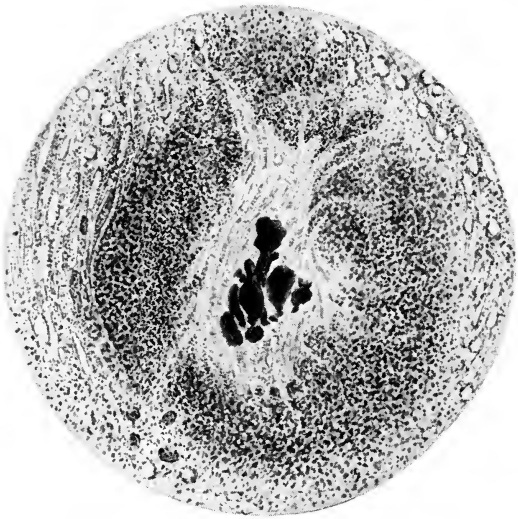
IN THE SUMMER SESSION OF 1895

BOSTON, U.S.A., AND LONDON
GINN & COMPANY, PUBLISHERS
The Athenæum Press
1896

CONTENTS.

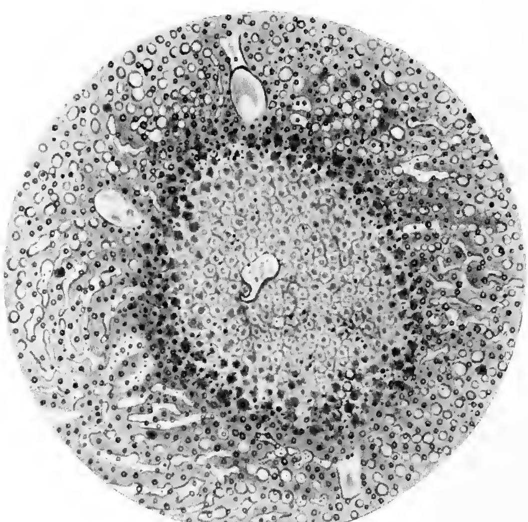
Biol. Lect., to face page 1.

FIG. I.



Experimental Abscess in the Kidney of the Rabbit.
Staphylococcus pyogenes aureus infection.

FIG. II.



Experimental focal cell necrosis in the liver of the Guinea pig. Ricin intoxication.

FIRST LECTURE.

INFECTION AND INTOXICATION.

SIMON FLEXNER, M.D.

(ASSOCIATE PROFESSOR OF PATHOLOGY, JOHNS HOPKINS UNIVERSITY.)

THE science of biology in its widest sense comprises the study of life in all its forms and activities, both normal and abnormal. For this reason I shall not apologize for bringing before you a subject closely related to pathology, a branch which is concerned only with the abnormal forms and activities of life.

The underlying principles, which are to-day the subjects of thought and research in the branches usually classed as the biological sciences, are not essentially different from those which are also found in the field of work which more peculiarly belongs to pathology. Nor is pathology any longer a study, the subject matter of which is limited to man and the higher animals. Its application to the lower animals, and even to plants, has been so successful that we are now justified in looking to the comparative study of disease processes for the solution of some of the many still obscure problems in human pathology.

Manifestly it would be neither possible nor profitable to attempt to compass in so brief a time the entire field of pathological research. It becomes necessary, therefore, to restrict our attention to a single one of its problems; and as there is at the present time none which is attracting more attention than that relating to the causation and effects of infectious diseases, I have chosen for this hour the discussion of one aspect of this subject. My remarks will be prefaced with a few general statements concerning the parasitic agents of disease. Some of these belong to the vegetable, others to the animal kingdom. They are found in the former, among the fungi and bacteria, and in the latter, among the protozoa, vermes, and arthropods. While, however, the term pathogenic micro-organisms is arbitrarily applied to all the vegetable parasites, among the animal parasites only the protozoa should properly come under this category.

Infectious diseases, then, are such as are caused by pathogenic micro-organisms, *i.e.* by fungi, bacteria, and protozoa. In speaking of the bacterial origin of diseases many writers apply the term bacteria to micro-organisms of animal as well as of vegetable origin; but it must be remembered that protozoa are not bacteria, although the term pathogenic micro-organisms can be properly applied to both. I wish, therefore, to emphasize the fact, that besides the diseases of bacterial origin, there are also others which are caused by organisms belonging to the animal kingdom. Typical examples of this class are found in the different forms of malarial fever which are caused by the invasion of the blood and organs by organisms belonging to the group of protozoa.

It must, however, be admitted that the diseases caused by vegetable parasites are best understood. This fact is easily explained by our present successful methods employed for the propagation of these parasites outside the body, whereas as yet the pathogenic protozoa have not been obtained in the form of pure cultures outside the bodies of infected animals. The growth and multiplication of the pathogenic micro-organisms are associated in many instances with the production of certain substances of a toxic nature, these poisons, or toxins as they are called, playing a great rôle in the causation of disease. Certain non-pathogenic or saprophytic micro-organisms in the course of their growth are also capable of producing poisonous products. There is, however, this marked difference between these two classes of agents, namely, that whereas the former are capable of living and of manufacturing the toxins within the living body, the latter can subsist only in the presence of dead material. Examples of poisoning by the products developed by saprophytic bacteria are found in the accounts, which we so often read, of epidemics occurring suddenly to large numbers of persons from the ingestion of partly decomposed meat, fish, sausage, milk, etc. Infection is therefore to be distinguished from intoxication, inasmuch as the first presupposes the existence of a living agent which enters the body and survives there, while the second is to be attributed to the effects of any toxic agent which may be present in the body in sufficient amount to produce more or less marked symptoms of disease. The relation of intoxication to infection cannot be better expressed than in the following paragraph. "It is impossible to draw any sharp dividing line between intoxication and infection; but it is believed to conduce to precision and clearness to regard as agents of infection only such as are capable of reproduction, that is, such as are living organisms and not include among these agents chemical poisons whether produced by bacteria or other vegetable cells or by animal cells" (Welch).

There is perhaps a tendency at the present time to minimize the importance of the living agents themselves in the production of the phenomena of infectious disease, and to ascribe these entirely to the action of the toxic agents manufactured by the micro-organisms. But in view of the fact that in several typical infectious diseases, among which may be mentioned anthrax, asiatic cholera, and typhoid fever, it has been found quite impossible to separate in an active form the toxic products from the bacteria which produce them, the latter cannot be regarded as less essential to the production of the disease than the former. Indeed there are few diseases at present known in which all the symptoms can be ascribed to the toxic products of the micro-organisms alone. To quote another paragraph from Dr. Welch's writings: "In the case of most infectious diseases we can no more separate the actual presence, multiplication, and specific vital activities of the bacteria within the body from the disease than we can substitute any chemical substance for the actual presence and growth of the yeast fungi in the production of alcohol from sugar."

Yet the rôle played by the chemical substances developed from certain bacteria in the production of the phenomena of disease is not inconsiderable, and we may safely say that only with such bacteria as produce toxins of great potency, which are easily yielded by the cells to the surrounding medium, would it be possible in a given disease for the toxic chemical substances by themselves to give rise to the same phenomena as those which are due to the action of the living bacteria.

The study of the nature and action of these toxins, or, as they are now generally called toxalbumins, has added not a few interesting facts to our knowledge of poisons in general; but, at the same time, it must be understood that the forms with which we are dealing have not at this time been isolated in a state of absolute purity, although they have been obtained in a condition of great potency. Their exact nature is not as yet well understood. They are believed by most bacteriologists and chemists to be of an albuminous nature, many authorities claiming them as enzymes. They are amorphous bodies and differ essentially from the crystallizable ptomaines, with which substances they are sometimes confused. Perhaps the one best studied, certainly the one possessing the greatest potency, is the toxalbumin produced by the tetanus bacillus. In the still impure state in which it has been obtained, its activity has been found to be simply appalling. A single dose of 0.000.000.05 grm. suffices to produce death after tetanic convulsions in a mouse weighing 15 grams, and it is estimated that the fatal dose for an adult human being does not exceed 0.23 mg. You will appreciate this fact better if you remember that the fatal dose of atropine is 130 mg., and of strychnia from 30 to 100 mg. It should further be mentioned that this toxalbumin, unlike many of the others, is capable of giving rise to the same symptoms as the bacillus which produces it.

Another extremely virulent, although less active, toxalbumin is that obtained from the cultures of the diphtheria bacillus. Of this 0.4 mg. suffices to kill eight guinea pigs, each weighing 400 grams.

In contradistinction to the tetanus toxin, that produced by the diphtheria bacillus does not reproduce the entire series of phenomena of the disease to which it belongs, since the injection of it does not produce at the point of inoculation an actual false membrane. An extraordinary feature exhibited by the diphtheria toxin is seen in the extreme slowness with which it is sometimes known to act. Whereas the poisonous chemical agents with which we were previously acquainted exert their effect quickly, and usually after a short interval, the diphtheria toxin requires at times weeks and even months for the production of fatal results in the animal inoculated. For a time it stood alone in this regard, but I have found similar delay in the action of another toxalbumin, — ricin, a substance yielded by the seeds of the ricinus communis (castor plant).

Recent studies have shown that the toxalbumins are widely distributed in nature. Thus far they have been found among the lower and higher vegetable forms, and even in the blood of various animals, such as the eel, snake, and dog.

When we proceed to study the effects of these pathogenic agents upon the animal body, we find that the phenomena which are caused by the toxins can often be distinguished from those due to the actual presence of the bacteria themselves.

Two main forms of lesions of cells can be distinguished in infectious diseases. In the one, most or all of the cells are affected; the lesion is diffuse, and shows itself by an increase in the size and granulations of the cells, associated often with the appearance of globules of fat in those otherwise free from this substance, or with an increase of it in those already containing it. In this way is brought about the so-called parenchymatous degeneration of cells, which in extreme cases may lead to actual cell death (necrosis). This is the typical lesion ascribed to the action of chemical substances. It is found in all infectious diseases and in many forms of intoxication.

More interesting are the so-called focal lesions, of which it may be said that certain ones are caused by bacteria and others by toxic substances. As an example of the former, a small abscess may be taken. The bacteria which are most commonly associated with this pathological process are cocci, which grow in grape-like clusters presenting often, when cultivated on artificial media, a golden-yellow color, whence the name "Staphylococcus pyogenes aureus." If a section be made through such an abscess (Fig. 1), which is located, as so commonly happens in experimental cases, in the kidney, the following arrangement is found. The central dark mass represents the bacteria which have been transported hither by the blood current, and which have become lodged in the capillary vessels of the part. Having found here conditions favorable to their increase, they have grown from a microscopic speck to a mass large enough to be seen with the naked eye. As a result of their presence, the surrounding tissue is destroyed, the destruction being recognizable in the specimen by the absence of stainable nuclei in this part. Outside the zone of dead tissue is another in which the cells as compared with those of the healthy tissue at a distance are greatly increased in number. This third zone is the area of leucocytic infiltration, the infiltrating cells consisting of white blood-corpuscles which have passed out of the vessels to accumulate at this spot in answer to what is conceived to be a chemical attraction (chemotropism) exerted by the bacteria and dead tissue. The leucocytes penetrate as far as possible into the dead tissue, and become arrested as soon as the poisonous products of the bacteria are present in quantities sufficient to insure their speedy destruction. Later a solvent action is exerted by the bacteria upon the tissues, causing them to liquefy, and converting the contents into "pus," the removal of which leaves a cavity behind.[1]

Certain bacteria are capable of exerting an injurious effect upon tissues and organs of the animal body at a greater distance from their place of localization. Thus, although the diphtheria bacillus often remains localized in the throats of persons suffering from diphtheria, yet very extensive local lesions are found in the near and remote lymphatic glands, in the spleen, liver, heart, nerves, and other organs. These lesions are attributable to the absorption into the body of the toxalbumin, elaborated by the bacteria in the throat. It is

[1] It is not to be concluded that this is the only kind of lesion produced by bacteria. It is a common one, and has been selected for that reason, and also because, as far as known, it is never produced by the action of the toxic products of bacteria alone.

indeed possible by using the bodies of susceptible guinea pigs and rabbits to show that identical pathological changes can be produced by inoculation with the toxalbumin alone. A closer study of the lesions shows them to be different from those caused by the pus-producing cocci. Such a lesion in the liver of the guinea pig, resulting from diphtheria intoxication, is shown in Fig. 2. Note here that a destruction of cells has taken place, but that no bacteria are to be seen in the neighborhood of the dead cells. The cells themselves present a different appearance from those seen in the kidney abscess. Individually they are better preserved ; their outlines are sharper, and they are more easily made out than the normal cells. Examined in the fresh state, in physiological salt solution, they present a characteristic glassy appearance, whence the term "hyaline," which is often applied to them. That they are necrotic is shown not only by the behavior of their protoplasm in the presence of staining agents, but also by the absence of normal nuclei in them. For the most part, the nuclei have entirely disappeared, but here and there a shrunken one can be seen, and occasionally small pigmented fragments are still preserved. The intensity of the process evidently grows less as one proceeds from the center to the periphery of such a focus, and at the extreme edge a variable number of leucocytes are encountered. They are never accumulated in quantities, such as are seen in abscess formation, and such a lesion shows no tendency to undergo softening with the production of an abscess or cavity.[1]

With respect to the toxalbumins which are derived from the higher plants (ricin, abrin), I have found that the pathological lesions which they cause are similar, if not identical, with those produced by the toxalbumins of bacterial origin.

Besides the toxins of vegetable origin, toxic proteid substances, some of which are of great potency, are yielded by the animal kingdom. Among these have already been mentioned

[1] When it is considered that these toxins are soluble substances, and presumably in perfect solution in the body fluids, the explanation of their tendency to produce focal effects is not at once evident. Several hypotheses have been advanced to account for this phenomenon. See "The Pathological Changes Caused by Certain So-called Toxalbumins." *Medical News*, Phila., Aug. 4, 1894.

the toxic constituents of snake venom and the blood of certain animals. The poisonous effects of snake venom are familiar to you; but it is less generally known that the blood of one species of animal, freed from its corpuscular elements, may exhibit poisonous properties when introduced in sufficient amounts into an animal of a different species. Thus the blood serum of human beings, and of the dog, is highly poisonous to the rabbit, and that of the lamb to human beings.

In the course of my studies in this direction, I have been able to show that the injurious effects which the blood of one animal produces in another is due to the toxic substances contained in the foreign blood, and not alone to the destruction of the blood-corpuscles of the host which commonly ensues. This latter phenomenon is spoken of as the globulicidal in contradistinction to the toxicidal effects of the foreign serum, and when the amount of foreign serum introduced into a susceptible animal is very large, the destruction of corpuscular elements may be great enough to cause immediate death. The toxicidal effect is produced much more slowly. The toxic constituents of the blood serum obtained either from the dog or from human beings bring about in the tissues of the rabbit changes similar to those caused by the vegetable toxalbumins which have been considered.

Having now seen that these agents of intoxication, whether derived from animal forms of low or high position, or from vegetable life high or low in point of organization, possess certain features in common and produce similar pathological effects when tested upon susceptible animals, it will be of interest to extend a little further our inquiry into their properties.

Among the most interesting of these from a theoretical, and of the greatest significance from a practical standpoint, are the effects of small and repeated doses of these substances. The facts elicited by the study of the effects produced by these bodies when introduced into certain animals in this way have an important bearing upon the questions of insusceptibility to disease in general, and are included in the subject matter of immunity.

The production of immunity to many bacteria or their products is associated with the formation in the animal thus protected of certain antidotal substances which appear in the body fluids. It has been shown that a similar immunity for ricin and abrin can be induced, and more recently the same has been proved for snake venom. In these instances the insusceptibility to the actions of the toxic agents is associated with the appearance in the blood of the treated animals of antidotal bodies capable of affording protection from these toxic proteids. In this connection, I have been able to show that by the exhibition of repeated small doses, rabbits, otherwise highly susceptible, can be made quite resistent to the blood serum of the dog.

The foregoing considerations teach that, in the study of the causation of disease, a widening knowledge is enabling us to appreciate how much is due to the actions of the living parasitic agents themselves, and how much to toxic substances derived from these and from other sources. The importance of agents of intoxication is becoming more and more impressed upon us; and when we reflect that their distribution is coextensive with organized nature itself, and that they are present in the most vital of our body constituents, we begin to see, if indeed only faintly, what consequences their presence may entail.

I would bring these remarks to a close by begging you not to forget that although much has been written upon the disease-producing micro-organisms, not a small chapter might be added upon those which are friendly in their nature. When you consider that the phenomena of decomposition and putrefaction are executed through their efforts, that the restoration of the soil, and the fitting of it for the growth of the higher plants, is effected by a special group of bacteria, you will appreciate the fact that life on this globe would be impossible for the higher living forms could these lowly ones be perchance exterminated.

Furthermore, there are defences set up everywhere in the animal body through which the invasion of these noxious parasites is resisted. Those parts most exposed to their action are either covered by a dense and relatively impenetrable membrane, or if protected by a barrier less secure, are bathed with fluids at once injurious to them, and offering mechanical obstacles to their settlement. Thus for the exterior of the body we have as a rampart, the skin, and for each orifice its mucous surface with its own peculiar secretion. Even should the parasite be able to pass beyond these outposts, its fate is still insecure, for the lymphatic tissues stand as a closed gateway to oppose its further progress; and beyond these again are forces still more impregnable, — the body fluids and cells, which are capable of destroying large numbers of bacteria, and probably no inconsiderable quantities also of their toxic products.

SECOND LECTURE.

IMMUNITY.

BY GEORGE M. STERNBERG, M.D., LL.D.

(Surgeon-General U. S. Army, Washington, D. C.)

The resisting power, natural or acquired, which living animals possess against invasion by pathogenic micro-organisms is commonly spoken of as "immunity." But we might include in our definition of the term, used in the biological sense which we shall attach to it in the present lecture, the more general resisting power which living animals possess against saprophytic bacteria. It is hardly necessary to call attention to the fact that, under suitable conditions as to temperature and moisture, dead animal tissues undergo putrefactive decomposition,—*i.e.* are invaded by saprophytic bacteria,—while healthy, living animals resist such invasion. This more general immunity appears to be due to causes which are the same or similar to those which enable insusceptible animals to resist invasion by pathogenic bacteria. There is also an immunity, which the Germans designate "*giftfestigung*," which is manifested by an increased resisting power to the toxic action of the chemical products of pathogenic bacteria, and which may be established by introducing these toxic substances into susceptible animals quite independently of the micro-organisms which produce them — inoculations with filtered or sterilized cultures. This corresponds with the acquired immunity which has been shown to result from the inoculation of susceptible animals with non-lethal doses of certain toxic albuminous substances of animal and vegetable origin, — snake poison, abrin, ricin, etc.

By "natural immunity" we mean the insusceptibility which certain species or certain individuals have against infection by certain pathogenic bacteria. "Acquired immunity" is the resisting power which results, in originally susceptible animals, from a non-fatal attack of an infectious disease, or from protective inoculations with "attenuated" or filtered cultures of pathogenic bacteria.

As is well known, certain infectious diseases are peculiar to man, certain others to one or more species of lower animals, and others still may be transmitted from man to certain lower animals, or *vice versa*. Thus typhoid fever, yellow fever, cholera, measles, etc., are infectious diseases of man, and during their epidemic prevalence the lower animals show no evidence of susceptibility to infection. On the other hand, Texas fever and infectious pleuropneumonia, which are very fatal to cattle, hog cholera and swine plague, chicken cholera, etc., are never communicated to those who care for the infected animals; in other words, man has a natural immunity against these diseases. Again, certain infectious diseases are common to man and to certain species of the lower animals. Thus, tuberculosis may be transmitted to monkeys, to cattle, rabbits, guinea pigs, and fowls; carnivorous animals in confinement, also, sometimes succumb to tubercular infection. Anthrax is fatal to cattle, sheep, and small herbivorous animals, and may be transmitted to man by inoculation, or by the introduction of dry spores into the respiratory passages — "woolsorter's disease." Diphtheria may be transmitted to cats and fowls, and cultures of the diphtheria bacillus are extremely pathogenic for the guinea pig. Glanders, which is a disease of the equine genus, may be transmitted to man, to the guinea pig, and to the field mouse; but house mice have a natural immunity against infection by this bacillus. On the other hand, field mice and guinea pigs are not susceptible to infection by the Bacillus erysipelatus suis, which is very fatal to house mice, white mice, rabbits, swine, sparrows, and pigeons. There are also differences in susceptibility to various infectious diseases among different races of the same species. Thus the Algerian sheep has an immunity against anthrax; Texas cattle, as a rule, do not succumb to Texas fever, which is very fatal to northern cattle; yellow fever is much less fatal to the negro than to the white race; the negro also resists malarial infection better than the white. In general, carnivorous animals have but slight susceptibility to the various forms of infectious septicæmia which are fatal to the herbivora. The introduction beneath the skin of a mouse or a rabbit of a little putrefying flesh infusion frequently gives rise to a fatal septicæmia, due to the presence of one or more species of bacteria pathogenic for these animals, but harmless for the carnivora which prey upon them. Were this otherwise, the carnivora would be destroyed by wounds inflicted in their fights over animals which had died of infectious diseases or which were in a state of putrefaction. It appears probable that the immunity of the carnivora to the infectious septicæmias referred to has been acquired in process of time by natural selection — survival of the fittest.

Besides the race immunity referred to, we have differences in the degree of susceptibility to various infectious diseases in individuals of the same race. Some individuals or families have manifestly a special susceptibility to tubercular infection; others are especially subject to contract smallpox, as shown by the occurrence of two or more attacks in the same individual. Susceptibility also depends to some extent upon age. The young are especially susceptible to scarlet fever, whooping cough, and diphtheria. In the lower animals, we find that an "attenuated virus" which will not kill an adult of a susceptible species may prove fatal to a very young animal of the same species.

Immunity, whether natural or acquired, in many cases has only a relative value, and may be overcome by an excessive dose or by unusual virulence of the infectious material. This is true, for example, of the natural immunity of the Algerian race of sheep as regards anthrax, of the acquired immunity resulting from vaccination against smallpox, etc. But it does not apply in the case of animals which have a complete natural immunity for infectious diseases peculiar to other species. Thus man never contracts swine plague or infectious pleuropneumonia under any circumstances, and domestic animals never contract yellow fever or cholera during the epidemic prevalence of these diseases.

The relative immunity, natural or acquired, to diseases which are not strictly limited to a single species, may often be overcome by various agencies acting upon the individual exposed to infection. Thus Arloing was able to induce symptomatic anthrax in animals naturally immune for this disease by mixing with his cultures various chemical substances, such as carbolic acid, pyrogallic acid, and especially lactic acid (twenty per cent). Leo has shown that white mice, which are not subject to the pathogenic action of the glanders bacillus, may be rendered susceptible by feeding them for some time upon phloridzin, which gives rise to an artificial diabetes, and causes the tissues to become impregnated with sugar. Behring claims to have demonstrated by experiment that white rats lose their immunity for anthrax when fed for some time upon an exclusively vegetable diet, or when phosphate of lime is added to their food; and he has suggested that the immunity of these animals may be due to the highly alkaline reaction of their blood and tissue juices. Nocard and Roux found by experiment that an attenuated culture of the anthrax bacillus, which was not fatal to guinea pigs, killed these animals when injected into the muscles of the thigh after they had been bruised by mechanical violence. Abarrin and Roger found that white rats, which are not susceptible to anthrax, became infected and frequently died if they were exhausted, previous to inoculation, by being compelled to turn a revolving wheel for a considerable time. Pasteur found that fowls, which have a natural immunity against anthrax, become infected and perish if they are subjected to artificial refrigeration after inoculation. This has been confirmed by the more recent experiments of Wagner (1891). According to Canalis and Morpurgo, pigeons which are enfeebled by inanition easily contract anthrax as a result of inoculation. Arloing states that sheep which have been freely bled contract anthrax more easily than others; and Serafini found that when dogs were freely bled, the bacillus of Friedländer, injected into the trachea or the pleural cavity, entered, and apparently multiplied to some extent in the blood, whereas without such previous bleeding they were not to be found in the circulating fluid. Certain anæsthetic agents have also been shown to produce a similar result. Platania communicated anthrax to immune animals — dogs, frogs, pigeons — by bringing them under the influence of curare, chloral, or alcohol; and Wagner obtained similar results in his experiments upon pigeons to which he had administered chloral. In man, clinical experience shows that those who are addicted to the excessive use of alcohol are especially liable to contract certain infectious diseases, — pneumonia, erysipelas, yellow fever, etc.

The pathogenic potency of known disease germs varies as widely as does the susceptibility of individuals to their specific action. In general it may be said that the more recently the germ comes from a developed case of the disease to which it gives rise, the more virulent it is, and the longer it has been cultivated outside of the animal body, the more attenuated is its pathogenic power. Thus, when the discharges of a typhoid-fever patient find their way directly to a water-supply of limited amount, a large proportion of those who drink the water are likely to be attacked; but when a considerable interval of time has elapsed since the contamination occurred, although the germs may still be present, the liability to attack is much less, on account of diminished pathogenic virulence.

What has been said thus far indicates that infection depends (*a*) upon the susceptibility of the individual (predisposition), (*b*) upon the virulence of the infectious agent, and (*c*) upon the quantity introduced to a vulnerable point, — *e.g.* beneath the skin by inoculation or through an accidental wound in anthrax and other forms of septicæmia, into the alimentary canal in typhoid fever and cholera, or into the respiratory passages in diphtheria, influenza, pneumonia, and pulmonary tuberculosis. Still another factor may be called into play. In addition to the specific cause or germ, and the natural or acquired (by various depressing agencies referred to) predisposition, a direct exciting cause may be necessary to establish a localized infectious process. Thus, catching cold may be the exciting cause which develops an attack of pneumonia or influenza or tuberculosis in an individual having a predisposition to these diseases, — the specific cause being present; or indigestible food in the *primae viae* may be the exciting cause of an attack of cholera; or the irritation resulting from breathing an atmosphere loaded with dust may give rise to tubercular infection. Again, bruising of the tissues may give rise to an abscess or a carbuncle in an individual whose vital resisting power is below par, the specific agents of such local infections (the pus cocci) being widely distributed and frequently found on the surface of the body and upon exposed mucous membranes in healthy individuals.

A non-fatal attack of an infectious malady, as a rule, is followed by a relative immunity of longer or shorter duration. In smallpox, scarlet fever, measles, yellow fever, typhoid fever, and certain other diseases of man one attack usually protects during the life of the individual; but exceptions to this rule are not rare, especially in the case of smallpox. In pneumonia, diphtheria, influenza, and cholera second attacks are frequent; and while a relative degree of immunity is no doubt acquired as a result of an attack, this is of brief duration.

The production of immunity by protective inoculations was for a long time limited to a single disease, — smallpox. Inoculations with virus, obtained from a pustule on a smallpox patient, were extensively practised before the discovery of vaccination by Jenner. These inoculations gave rise to a mild attack of the disease, followed by immunity, which was apparently as complete as that following a more severe attack contracted in the usual way. This method seems to have been practised by eastern nations long before it was introduced into Europe. It was extensively employed in Turkey early in the eighteenth century, and was introduced into England through the influence of Lady Mary Wortley Montagu. No doubt the mortality from smallpox was greatly diminished by these inoculations; but they were attended by the disadvantage that the disease was propagated by them, inasmuch as inoculated individuals became a source of infection for others. Inoculation was still practised in England for some time after the demonstration of the protective value of vaccination, but in 1840 it was prohibited by an act of Parliament.

There is some evidence that vaccination as a protection against smallpox was practised to a limited extent prior to the time of Jenner. Thus Von Humboldt has stated that it was known at an early period to the Mexicans. But its introduction as a reliable method of protecting against smallpox is due to the patient researches of the renowned English physician, whose attention was first attracted to the subject in 1768, although it was not until 1796 that he made his first vaccination in the human subject. His first public institution for the practice of vaccination was established in 1799, and the following year the practice was introduced into France, Germany, and the United States.

In the infectious disease of cattle known as pleuropneumonia, protective inoculations were successfully made some time before the demonstration by Pasteur of the efficacy of such inoculations in anthrax and chicken cholera (1880). Various methods have been employed. Thus Willems states that the natives of the banks of the Zambeze cause animals to swallow a certain quantity of the liquid from the pleural cavity of an animal recently dead, and thus give them immunity. The virus has been injected into the circulation by some experimenters, and others have proposed to attenuate it by heat. But the method which has been most extensively employed is that discovered by the Dutch settlers at the Cape of Good Hope (the Boers), and consists in inoculating animals in the tail with serum from the lungs of an animal recently dead, or with a virus obtained from the tumefaction produced by such an inoculation in the tail. This secondary virus was very extensively used by Lenglen, a veterinarian at Arras, who communicated his results to the Academy of Science at Paris, in April, 1863, and Willems says, in his last published communication, that this is the method which he prefers. It is also the method most extensively employed in Australia, into which country infectious pleuropneumonia was introduced in 1858.

Toussaint, a pioneer in researches relating to protective inoculations, has a short paper in the *Comptes-Rendus* of the

French Academy of Sciences of July 12, 1880, entitled "Immunity from Anthrax ('charbon') Acquired as a Result of Protective Inoculations."

In this paper he announces his discovery of the important fact that the anthrax bacillus does not form spores in the tissues or liquids of the body of an infected animal, but multiplies alone by binary division, — "sa multiplication se fait toujours par une division du mycélium."

In the same communication he reports his success in conferring immunity upon five sheep by means of protective inoculations, and also upon four young dogs. We must, therefore, accord him the priority in the publication of experimental data demonstrating the practicability of accomplishing this result.

But it is especially to the experimental researches of Pasteur that we are indebted for the development of practical methods, which have been extensively employed in protecting cattle, sheep, and swine from the fatal effects of various infectious maladies, and man from hydrophobia as the result of the bite of a rabid animal.

Pasteur's inoculations are made with an "attenuated virus," — *i.e.* with a culture of a pathogenic micro-organism which has a diminished degree of virulence and which when introduced into a susceptible animal induces a non-fatal and comparatively mild attack.

The researches of Pasteur and of his followers in this line of investigation show that pathogenic virulence may be attenuated by prolonged exposure to oxygen; by exposure to a temperature a little below that which would completely destroy vitality; by the action of certain chemical agents; and in some cases, by passing through a series of non-susceptible animals.

As a general rule pathogenic virulence is increased by successive inoculations in susceptible animals and diminished by cultivating the pathogenic micro-organism in artificial media outside of the animal body or by passing it through animals having but slight susceptibility to its pathogenic action. As pathogenic virulence depends, to a considerable extent at least, upon the formation of toxic substances during the active development of the pathogenic micro-organism, we infer that diminished virulence is due to a diminished production of these toxic substances.

An important step was made in the progress of our knowledge in this field of research when it was shown that animals may be made immune against certain infectious diseases by inoculating them with filtered cultures, containing the toxic substances just referred to, but free from the living bacteria to which they owe their origin. The first satisfactory experimental evidence of this important fact was obtained by Salmon and Smith in 1886. These bacteriologists succeeded in producing an immunity in pigeons against the pathogenic effects of the bacillus of hog cholera, which is very fatal to these birds, by inoculating them with sterilized cultures of the bacillus mentioned. Similar results were reported by Roux in 1888, from the injection into susceptible animals of sterilized cultures of the anthrax bacillus, and also of the bacillus of symptomatic anthrax. More recently (1890) Behring and Kitasato have shown that animals may be made immune against the pathogenic action of the bacillus of tetanus or the bacillus of diphtheria by the injection of filtered, germ-free cultures of these bacilli. Similar results have been obtained by G. and F. Klemperer (1891), in experiments upon rabbits, with filtered cultures of the micrococcus of croupous pneumonia.

In Pasteur's protective inoculations against hydrophobia it is probable that the immunity which is developed after infection by the bite of a rabid animal is due to the toxin (toxalbumin ?) of this disease present in the emulsion of spinal cord which is used in these inoculations.

There is also some evidence to show that a certain degree of immunity against tuberculosis may be produced in guinea pigs by injections of the toxic substances developed during the growth of the tubercle bacillus, — Koch's tuberculin.

Explanation of Natural Immunity.

We have now to inquire upon what the natural immunity depends which enables the healthy animal body to resist invasion by the destructive agents referred to.

Phagocytosis. — In my chapter on "Bacteria in Infectious Diseases," in *Bacteria*, published in the spring of 1884, but placed in the hands of the publishers in 1883, I say: —

"It may be that the true explanation of the immunity afforded by a mild attack of an infectious germ disease is to be found in an acquired tolerance to the action of a chemical poison produced by the micro-organism, and consequent ability to bring the resources of nature to bear to restrict invasion by the parasite."

In the same chapter the resources of nature supposed to be brought to bear in restricting invasion by the parasite are referred to as follows: —

"If we add a small quantity of culture fluid containing the bacteria of putrefaction to the blood of an animal withdrawn from the circulation into a proper receptacle and maintained in a culture oven at blood-heat, we will find that these bacteria multiply abundantly, and evidence of putrefactive decomposition will soon be perceived. But if we inject a like quantity of the culture fluid, with its contained bacteria, into the circulation of a living animal, not only does no increase and no putrefactive change occur, but the bacteria introduced quickly disappear, and at the end of an hour or two the most careful microscopical examination will not reveal the presence of a single bacterium. This difference we ascribe to the vital properties of the fluid as contained in the vessels of a living animal, and it seems probable that the little masses of protoplasm known as white blood-corpuscles are the essential histological elements of the blood, as far as any manifestation of vitality is concerned. The writer has elsewhere (1881) *suggested that the disappearance of the bacteria from the circulation, in the experiments referred to, may be effected by the white corpuscles*, which, it is well known, pick up, after the manner of amœbæ, any particles, organic or inorganic, which come in their way. And it requires no great stretch of credulity to believe *that they may, like an amœba, digest and assimilate the protoplasm of the captured bacterium, thus putting an end to the possibility of its doing any harm.*

"In the case of a pathogenic organism we may imagine that, when captured in this way, it may share a like fate if the captor is not paralyzed by some potent poison evolved by it, or overwhelmed by its superior vigor and rapid multiplication. In the latter event the active career of our conservative white corpuscles would be quickly terminated and its protoplasm would serve as food for the enemy. It is evident that in a contest of this kind the balance of power would depend upon circumstances relating to the *inherited* vital characteristics of the invading parasite and of the invaded leucocyte."

This explanation is now very commonly spoken of as the "Metschnikoff theory," although, as shown by the above quotations, it was clearly stated by the writer several years (1881) before Metschnikoff's first paper (1884) was published. Metschnikoff has, however, been the principal defender of this explanation of acquired immunity, and has made extensive and painstaking researches, as a result of which many facts have been brought to light which appear to give support to the present writer's hypothesis, — the so-called Metschnikoff theory.

The time at my disposal will not permit me to review the experimental evidence for and against the view that phagocytosis is the principal factor in protecting animals from invasion by pathogenic bacteria. The conclusion which I have reached is stated in my recently published work on *Immunity, Protective Inoculation, and Serum-Therapy* as follows: —

"The experimental evidence submitted, considered in connection with the extensive literature relating to 'phagocytosis,' leads us to the conclusion that natural immunity is due to a germicidal substance present in the blood-serum which has its origin (chiefly, at least) in the leucocytes, and is soluble only in an alkaline medium; and that local infection is usually resisted by an afflux of leucocytes to the point of invasion, but that phagocytosis is a factor of secondary importance in resisting parasitic invasion; also that general infection, at least in some infectious diseases, is resisted, and in non-fatal cases overcome, by an increase in the number of leucocytes and in the alkalinity of the blood-serum, — which favors solution of the germicidal proteids contained in the polynuclear leucocytes."

Recent researches indicate that the principal factor in the production of acquired immunity is the presence in the blood of the immune animal of some substance capable of neutralizing the toxic products of the particular pathogenic micro-organism against which immunity exists, or of destroying the "germ" itself.

These substances are called antitoxins. As pointed out by Buchner in a recent paper, the antitoxins differ essentially from the so-called alexins, to which natural immunity is ascribed. The alexins are characterized by their germicidal and globulicidal action (they destroy both the red corpuscles and the leucocytes of animals belonging to a different species from that from which they have been obtained), and by their coagulability and instability — destroyed by sunlight and by a temperature of 50° to 55° C. On the other hand, the antitoxins best known (diphtheria and tetanus) have no germicidal or globulicidal action; they resist the action of sunlight and require a temperature of 70° to 80° C. for their destruction.

Our knowledge of the antitoxins dates from the experiments made in the Hygienic Institute of Tokio, by Ogata and Jasuhara, in 1890. These bacteriologists discovered the important fact that the blood of an animal immune against anthrax contains some substance which neutralizes the toxic products of the anthrax bacillus. When cultures were made in the blood of dogs, frogs, or of white rats, which animals have a natural immunity against anthrax, they were found not to kill mice inoculated with them. Further experiments showed that mice inoculated with virulent anthrax cultures did not succumb to anthrax septicæmia if they received at the same time a subcutaneous injection of the blood of an immune animal. Further, it was found that mice which had survived anthrax infection as a result of this treatment were immune at a later date (after several weeks), when inoculated with a virulent culture of the anthrax bacillus. In the same year (1890) Behring and Kitasato discovered that the blood of an animal which has an acquired immunity against tetanus or diphtheria, when added to a virulent culture of one or the other of these bacilli, neutralizes the pathogenic power of such cultures, as shown by inoculation into susceptible animals; and also that cultures from which the bacilli have been removed by filtration, and which kill susceptible animals in very small amounts, have their toxic potency destroyed by adding to them the blood of an immune animal, which is thus directly proved to contain an antitoxin,—which comparative experiments show not to be present in the blood of non-immune animals. In the experiments of Behring and Kitasato referred to, it was found that 5 c.c. of serum from the blood of an immune rabbit, mixed with 1 c.c. of a virulent filtrate of the tetanus bacillus, and allowed to stand for twenty-four hours, completely neutralized its toxic power, as shown by inoculations in mice: 0.2 c.c. of this mixture injected into a mouse was without effect, while 0.0001 c.c. of the filtrate, without such admixture, was infallibly fatal to mice. The mice inoculated with this mixture remained immune for forty or fifty days, after which they gradually lost their immunity. The blood or serum from an immune rabbit, when preserved in a dark, cool place, retained its power of neutralizing the tetanus toxalbumin for about a week, after which time it gradually lost this power. Behring and Kitasato have also shown that the serum of a diphtheria-immune rabbit destroys the potent toxalbumin in diphtheria cultures. It does not, however, possess any germicidal power against the diphtheria bacillus.

In 1891 G. and F. Klemperer published an important memoir, in which they give an account of their researches relating to the question of immunity, etc., in animals subject to the form of septicæmia produced by the micrococcus of croupous pneumonia. They were able to produce immunity in susceptible animals by introducing into their bodies filtered cultures of this micrococcus, and proved by experiment that this immunity had a duration of at least six months. They also arrived at the conclusion that the immunity induced by injecting filtered cultures into susceptible animals is due to the production of an antitoxin in the body of the animal.

Brieger, Kitasato, and Wassermann have reported (1892) their success in conferring immunity upon guinea pigs against the pathogenic action of the cholera spirillum. They found that attenuated cultures suitable for use as "vaccines" could be obtained by cultivating the spirillum in bouillon made from the thymus gland of the calf, by which means they have also obtained attenuated cultures of the bacillus of diphtheria, the bacillus of typhoid fever, the bacillus of tetanus and the streptococcus of erysipelas. Guinea pigs inoculated with a culture in thymus bouillon, which had been subjected to a temperature of 65° C. for fifteen minutes, were found after twenty-four hours to be immune against virulent cultures in twice the amount which would otherwise have been fatal.

During the past two or three years numerous additional experiments have been reported which confirm the results already referred to, and show that immunity may be produced in a similar manner against the toxic products of various other pathogenic bacteria, — the typhoid bacillus, the "colon" bacillus, streptococcus pyogenes, staphylococcus pyogenes aureus and albus, etc.

The Italian investigators, Tizzoni and Centanni, in 1892, published a preliminary communication in which they gave the results of experiments which appear to show that in guinea pigs treated with tuberculin, by Koch's method, a substance is developed which neutralizes the pathogenic potency of the tubercle bacillus. Professor Tizzoni and his associate, Dr. Schwarz, have also (1892) obtained evidence that there is an antitoxin of rabies. Blood-serum taken from a rabbit having an artificial immunity against this disease was found to neutralize *in vitro* the virulence of the spinal marrow of a rabid animal after a contact of five hours. The blood-serum of dogs having an acquired immunity against rabies was found to have a similar action, but in much less degree. The substance (antitoxin) present in the blood-serum of an immune rabbit does not dialyze; it is precipitated by alcohol, and preserves its activity, to a considerable extent, after precipitation. It is soluble in glycerin, and is said to have the general characters of a "globulin." The experimenters named also succeeded in conferring immunity upon susceptible animals by injecting into them blood-serum containing this antitoxin. According to the Italian investigators named, the antitoxins of tetanus and of rabies are found only in the blood-serum of immune animals, and not in the tissues (nervous or muscular), or in the parenchyma of the various organs.

Professor Ehrlich, of Berlin, in 1891, published the results of some researches which have an important bearing upon the explanation of acquired immunity, and which show that susceptible animals may be made immune against the action of certain toxic proteids of vegetable origin, other than those produced by bacteria; also that this immunity depends upon the presence of an antitoxin in the blood-serum of the immune animals.

In a later paper (1892) Ehrlich has given an account of subsequent experiments which show that the young of mice, which have an acquired immunity for these vegetable toxalbumins, may acquire immunity from the ingestion of their mother's milk; and also that immunity from tetanus may be acquired in a brief time by young mice through their mother's milk. In his tetanus experiments Ehrlich used blood-serum from an immune horse to give immunity to the mother-mouse when her young were already seventeen days old. Of this blood-serum 2 c.c. was injected at a time on two successive days. The day after the injection one of the sucklings received a tetanus inoculation, by means of a splinter of wood to which spores were attached. The animal remained in good health, while a much larger control mouse, inoculated in the same way, died of tetanus at the end of twenty-six hours. Other sucklings, inoculated at the end of forty-eight hours and of seventy-two hours after the mother had received the injection of blood-serum, likewise remained in good health, while the control mice died.

The possibility of conferring immunity by means of the milk of an immune animal is further shown by the experiments of

Brieger and Ehrlich (1892). A female goat was immunized against tetanus by the daily injection of "thymus tetanus bouillon." The dose was gradually increased from 0.2 c.c. to 10 c.c. At the end of thirty-seven days a mouse, which received 0.1 c.c. of the milk of this goat in the cavity of the abdomen, proved to be immune against tetanus. Further experiments gave a similar result, even when the milk of the goat was not injected into the peritoneal cavity of the mouse until several hours after inoculation with a virulent culture of the tetanus bacillus.

In a subsequent communication (1893) Brieger and Ehrlich describe their method of obtaining the antitoxin of tetanus from milk in a more concentrated form. They found by experiment that it was precipitated by ammonium sulphate and magnesium sulphate. From twenty-seven to thirty per cent of ammonium sulphate added to milk caused a precipitation of the greater part of the antitoxin. This precipitate was dissolved in water, dialyzed in running water, then filtered and evaporated in shallow dishes at 35° C. in a vacuum. One liter of milk from an immune goat gave about 1 gm. of a transparent, yellowish-white precipitate, which contained fourteen per cent of ammonium sulphate. This precipitate had from four hundred to six hundred times the potency of the milk from which it was obtained in neutralizing the tetanus toxin.

A most interesting question presents itself in connection with the discovery of the antitoxins. Does the animal which is immune from the toxic action of any particular toxalbumin also have an immunity for other toxic proteids of the same class? The experimental evidence on record indicates that it does not. In Ehrlich's experiments with ricin and abrin he ascertained that an animal which had been made immune against one of these substances was quite as susceptible to the toxic action of the other as if it did not possess this immunity, — *i.e.* the antitoxin of ricin does not destroy abrin, and *vice versa.* As an illustration of the fact he states that in one experiment a rabbit was made immune for ricin to such an extent that the introduction into its eye of this substance in powder produced no inflammatory reaction; but the subsequent introduction of a solution of abrin, of 1 to 10,000, caused a violent inflammation. In this connection we may remark that there is some evidence to show that persons who are repeatedly stung by certain poisonous insects — mosquitoes, bees — acquire a greater or less degree of immunity from the distressing local effects of their stings.

We have also experimental evidence that animals may acquire a certain degree of immunity from the toxic action of the venom of the rattlesnake. This was first demonstrated by Sewall (1887), and has been recently confirmed by Calmette (1894).

The experimental evidence recorded justifies the conclusion that in the diseases referred to acquired immunity depends, chiefly at least, upon the presence of a peculiar proteid substance in the blood of the immune animal — antitoxin — which neutralizes the toxic substance — toxin or toxalbumin — to which the morbid phenomena which characterize the disease are due.

But it would be premature to infer that in all infectious diseases immunity depends upon the production of an antitoxin in the blood of the immune animal. Indeed, we have experimental evidence which shows that in certain cases the blood-serum of immune animals has no antitoxic power, but acts upon the germ itself, instead of upon its toxic products.

It may be worth while to refer briefly, before closing, to some examples of acquired immunity of a different order. We refer to the tolerance of extremes of heat and cold which may be established by habitual exposure, and more especially to the tolerance to narcotics and irritant poisons, which is very remarkable, and has never been explained in a satisfactory manner. A recent writer (Samuel, 1892) has presented experimental evidence which shows that the local inflammation which results from the application of croton oil to the ear of a rabbit does not occur when a second application is made to the same ear after recovery from the effects of the first. That a tolerance may be acquired to comparatively large doses of arsenic is well known, and the tolerance which the victims of drug habits acquire to enormous doses of narcotics is a matter of daily observation. In the writer's paper on acquired immunity, published in 1881, an attempt is made to account for acquired immunity in infectious diseases as analogous to the immunity to drugs just referred to. But it is evident that in the present state of science the analogy is incomplete, and possibly delusive, in the absence of any experimental evidence of the presence of specific antitoxins in the blood of those who, as a result of habit, tolerate excessive doses of morphia, cocaine, narcotin, etc.

THIRD LECTURE.

A STUDENT'S REMINISCENCES OF HUXLEY.

HENRY FAIRFIELD OSBORN.

(Columbia College, N. Y.)

By far the larger number of American students who go abroad pass through the English Channel, obtain a distant view of the mother country, and after from one to three years in Germany, return with an exclusively German education. Having visited neither England nor France, the implication is that the countries which produced Owen, Darwin, Huxley, Balfour, or Lamarck, Cuvier, St. Hilaire, and Pasteur have nothing to offer the American student. But this is not the fact. The fact is that England and France are a half-century behind Germany in that kind of university organization which attracts a foreign student, and enables him immediately to find his level and enter upon his research. English and French universities until a very recent date have been either not so fully prepared, or have met the newcomer with practically insuperable obstacles in the matter of a degree.

None the less, the student who has not breasted these obstacles for the compensating advantages which the English and French schools offer has made a serious mistake. He has brought back not an Old World education, but an exclusively German education, with its splendidly sound and unique features, and with many inherent defects. Germany produces the generals and the rank and file of the armies of science, but certainly the commanders-in-chief, in biology at least, have been Englishmen. If we find the highest exponents of purely inductive research in Germany, we certainly find a better union of the inductive and deductive methods in France and England. France leads in expression and style of thought, although, upon the whole, less sound in substance than Germany. England, and France in her best period, have given us the most far-reaching and permanent generalizations in biology. It follows that the American student who can afford the experience will profit most by placing himself successively in the scientific atmosphere of Germany, France, and England. My own post-graduate education was unfortunately not of this three-sided type. None the less, it has always seemed a most fortunate circumstance that in the spring of 1879 a letter from the venerable Kitchen Parker led me to Cambridge, and to the great privilege of sitting under Balfour, the most brilliant and lovable of men. In the following autumn Huxley's lectures upon Comparative Zoölogy began in October, and by entering this course I came to know personally this great master, and through him enjoyed the rare opportunity of meeting Charles Darwin. After this experience, which was equally open to any serious student of biology at that time, it is natural that I should strongly advise those of you who are planning your foreign studies to spend part of your time in England, and endeavor to discern some of the distinctive qualities of English men of science which Huxley so nobly illustrated. You will pardon the personal element in the following recollections of Huxley as a teacher, and the rather informal review of his life work.

Huxley, as a teacher, can never be forgotten by any of his students. He entered his lecture-room promptly as the clock was striking nine, rather quickly, and with his head bent forward "as if oppressive with its mind." He usually glanced attention to his class of about ninety, and began speaking before he reached his chair. He spoke between his lips, but with perfectly clear analysis, with thorough interest, and with philosophic insight which was far above the average of his students. He used very few charts, but handled the chalk with great skill, sketching out the anatomy of an animal as if it were a transparent object. As in Darwin's face, and as in Erasmus Darwin's or Buffon's, and many other anatomists with a strong sense of form, his eyes were heavily overhung by a projecting forehead and eyebrows, and seemed at times to look inward. His lips were firm and closely set, with the expression of positiveness, and the other feature which most marked him was the very heavy mass of hair falling over his forehead, which he would frequently stroke or toss back. Occasionally he would lighten up the monotony of anatomical description by a bit of humor. I remember one instance which was probably reminiscent of his famous tilt with Bishop Wilberforce at the meeting of the British Association in 1860. Huxley was describing the mammalian heart, and had just distinguished between the tricuspid valve on the right side of the heart and the bicuspid valve on the left, which you know resembles a bishop's miter, and hence is known as the mitral valve. He said, "It is not easy to recall on which side these respective valves are found, but I recommend this rule: you can easily remember that the mitral is on the left, because a bishop is never known to be on the right."

Huxley was the father of modern laboratory instruction; but in 1879 he was so intensely engrossed with his own researches that he very seldom came through the laboratory, which was ably directed by T. Jeffrey Parker, assisted by Howes and W. Newton Parker, all of whom are now professors, Howes having succeeded to Huxley's chair. Each visit, therefore, inspired a certain amount of terror, which was really unwarranted, for Huxley always spoke in the kindest tones to his students, although sometimes he could not resist making fun at their expense. There was an Irish student who sat in front of me, whose anatomical drawings in water color were certainly most remarkable productions. Huxley, in turning over his drawing-book, paused at a large blur, under which was carefully inscribed, "sheeps' liver," and smilingly said, "I am glad to know that is a liver; it reminds me as much of Cologne cathedral in a fog as of anything I have ever seen before." Fortunately the nationality of the student enabled him to fully appreciate the humor.

The greatest event in the winter of 1879 was Darwin's first and only visit to the laboratory. They came in together, Huxley leading slowly down the long narrow room, pointing out the especial methods of teaching which he had originated and which are now universally adopted in England and in this country. Darwin was instantly recognized by the class as he entered, and a thrill of curiosity passed down the room, for no one present had ever even seen him before. I remember my own feelings very distinctly. I was just finishing a laborious dissection of the lobster's nervous system, and out of politeness and deference to laboratory discipline, pretended to continue my work, with results fatal to the nervous system of the crustacean. As the pair came back up the room Huxley singled me out, I suppose because I was the only foreign student, and introduced me to Darwin, — the greatest kindness he could have shown a young student. There was the widest possible contrast in the two faces. Darwin's grayish-white hair and bushy eyebrows overshadowed the pair of deeply set blue eyes, which seemed to image his wonderfully calm and deep vision of nature, and at the same time to emit benevolence. Huxley's piercing black eyes and determined and resolute face were full of admiration and at the same time protection of his older friend. He said afterwards: "You know I have to take care of him — in fact, I have always been Darwin's bull-dog," and this exactly expressed one of the many relations which existed so long between the two men.

Huxley was not always fortunate in the intellectual caliber of the men to whom he lectured in the Royal School of Mines. Many of the younger generation were studying in the universities, under Balfour at Cambridge and under Rolleston at Oxford. However, Saville Kent, C. Lloyd Morgan, George B. Howes, T. Jeffrey Parker, and W. Newton Parker are representative biologists who were wholly trained by Huxley. Many others, not his students, have expressed the deepest indebtedness to him. Among these, especially, are Prof. E. Ray Lankester, of Oxford, and Prof. Michael Foster, of Cambridge. Huxley once said that he had "discovered Foster." He not only singled men out, but knew how to direct and inspire them to investigate the most pressing problems of the day. As it was, his thirty-one years of lectures would have produced a far greater effect if they had been delivered from an Oxford, Cambridge, or Edinburgh chair. In fact, Huxley's whole life would have been different, in some ways more effective, in others less so, if the universities had welcomed the young genius who was looking for a post, and even cast his eyes toward America in 1850; but in those early days of classical prestige both seats of learning were dead to the science, which it was Huxley's great service in support of Darwin to place beside physics, in the lead of all others in England. Moreover, Oxford, if not Cambridge, could not long have sheltered such a wolf in the fold.

Huxley's public addresses always gave the impression of being largely impromptu; but he once told me: "I always think out carefully every word I am going to say. There is no greater danger than the so-called *inspiration of the moment*, which leads you to say something which is not exactly true, or which you would regret afterward. I sometimes envy your countrymen their readiness, and believe that a native American, if summoned out of bed at midnight, could step to his window and speak well upon any subject." I told him I feared he had been slightly misinformed. I feared that many American impromptu speeches were more distinguished by a flow of language than of ideas. But Huxley was sometimes very impressive when he did not speak. In 1879 he was strongly advocating the removal of the Royal School of Mines from crowded Jermyn Street to South Kensington, — a matter which is still being agitated. At a public dinner given by the alumni of the school, who were naturally attached to the old buildings, the chairman was indiscreet enough to make an attack upon the policy of removal. He was vigorously applauded, when, to every one's consternation, Huxley, who was sitting at the chairman's right, slowly rose, paused a moment, and then silently skirted the tables and walked out of the hall. A solemn pall fell over the remainder of the dinner, and we were all glad to find an excuse to leave early.

In personal conversation Huxley was full of humor and greatly enjoyed stories at his own expense. Such was the following: "In my early period as a lecturer, I had very little confidence in my general powers, but one thing I prided myself upon was clearness. I was once talking of the brain before a large, mixed audience, and soon began to feel that no one in the room understood me. Finally I saw the thoroughly interested face of a woman auditor, and took consolation in delivering the remainder of the lecture directly to her. At the close, my feeling as to her interest was confirmed when she came up and asked if she might put one question upon a single point which she had not quite understood. 'Certainly,' I replied. 'Now Professor,' she said, 'is the cerebellum inside or outside of the skull?'" Once, speaking of his deafness, he said: "It is a great misfortune to be deaf in only one ear. Every time I dine out, the lady sitting by my good ear thinks I am charming, but I make a mortal enemy of the lady on my deaf side." A story of his about babies is also characteristic: "When a fond mother calls upon me to admire her baby I never fail to respond; and, while cooing appropriately, I take advantage of an opportunity to gently ascertain whether the soles of its feet turn in and tend to support my theory of arboreal descent."

Huxley's life is as full of suggestion to the student as were his lectures and his conversation. It illustrates the force of obtaining a very broad view of the animal kingdom before we attempt to enter the plane of higher generalization. Huxley's training in embryology, vertebrate and invertebrate zoölogy, palæontology, and geology was not mapped out for him as for the modern university student. His prolonged sea-voyage gave him time and material for reflection, and after this he was led from one subject to another until he obtained a grasp of nature as a whole, second only to that of Darwin.

Huxley was born in 1825. Like Goethe, he inherited from his mother his brilliantly alert powers of thought, and from his father, his courage and tenacity of purpose,—a combination of qualities which especially fitted him for the period in which he was to live. There is nothing striking recorded about his boyhood as a naturalist. He preferred engineering, but was led into medicine.

At the close of his medical course he secured a navy medical post upon the "Rattlesnake." This brought with it, as to Darwin, the training of a four-years' voyage to the South Seas off eastern Australia and west Guinea — a more liberal education to a naturalist than any university affords, even at the present day. This voyage began at twenty-one, and he says of it: "But, apart from experience of this kind and the opportunity offered for scientific work to me, personally, the cruise was extremely valuable. It was good for me to live under sharp discipline, to be down on the realities of existence by living on bare necessities, to find out how extremely worth living life seemed to be, when one woke from a night's rest on a soft plank, with the sky for a canopy, and cocoa and weevily biscuit the sole prospect for breakfast, and more especially to learn to work for what I got for myself out of it. My brother officers were as good as sailors ought to be and generally are; but, naturally, they neither knew nor cared anything about my pursuits, nor understood why I should be so zealous in the pursuit of the objects which my friends, the middies, christened 'Buffons,' after the title conspicuous on a volume of the *Suites a Buffon*, which stood in a prominent place on my shelf in the chart-room."

As a result of this voyage of four years, numerous papers were sent home to the Linnæan Society, of London, but few were published. Upon his return, his first work, *Upon the Anatomy and Affinities of the Medusæ*, was declined for publication by the Admiralty — a fortunate circumstance, for it led to his quitting the navy for good and trusting to his own resources. Upon publication (1849) this memoir at once established his scientific reputation at the early age of twenty-four, just as Richard Owen had won his spurs by his *Memoir on the Pearly Nautilus*. In 1852 Huxley's preference as a biologist was to turn back to physiology, which had become his favorite study in the medical course. But his fate was to enter and become distinguished in a widely different branch, which had as little attraction for him as for most students of marine life, namely, palæontology. He says of this sudden change of base:

"At last, in 1854, on the translation of my warm friend Edward Forbes to Edinburgh, Sir Henry de la Beche, the

Director-General of the Geological Survey, offered me the post Forbes had vacated of Palæontologist and Lecturer on Natural History. I refused the former point-blank, and accepted the latter only provisionally, telling Sir Henry that I did not care for fossils, and that I should give up natural history as soon as I could get a physiological post. But I held the office for thirty-one years, and a large part of my work has been palæontological."

From this time until 1885 his labors extended over the widest field of biology and of philosophy ever covered by any naturalist, with the single exception of Aristotle. In philosophy Huxley showed rare critical and historical power. He made the most exhaustive study of Hume, but his own philosophical spirit and temper was more directly the offspring of Descartes. Some subjects he mastered, others he merely touched; but every subject which he wrote about he illuminated. Huxley did not discover or first define protoplasm, but he made it known to the English-speaking world as the physical basis of life — recognizing the unity of animal and plant protoplasm. He cleared up certain problems among the *Protozoa*. In 1849 appeared his great work upon the oceanic *Hydrozoa*, and familiarity with these forms doubtless suggested the brilliant comparison of the two-layered gastrula to the adult hydrozoa. He threw light upon the Tunicata, describing the endostyle as a universal feature, but not venturing to raise the Tunicata to a separate order. He set in order the cephalopod mollusca, deriving the spiral from the straight-shelled fossil forms. He contributed to the Arthropoda, his last word upon this group being his charming little volume upon the *Crayfish*, — a model of its kind. But think of the virgin field which opened up before him among the vertebrata, when in 1859 he was the first to perceive the truth of Darwin's theory of descent. Here were Cuvier's and Owen's vast researches upon living and extinct forms, a disorderly chaos of facts waiting for generalization. Huxley was the man for the time. He had already secured a thoroughly philosophical basis for his comparative osteology by studying the new embryology of Von Baer, which Richard Owen had wholly ignored. In 1858 his famous

Croonian lecture on the "Theory of the Vertebrate Skull" gave the deathblow to Owen's life-work upon the skull and vertebral archetype, and to the whole system of mystical and transcendental anatomy; and now Huxley set to work vigorously to build out of Owen's scattered tribes the great limbs and branches of the vertebrate tree. He set the fishes and batrachia apart as the *Icthyopsidan* branch, the reptiles and birds as the *Sauropsidan* in contrast with the *Mammalian*, which he derived from a pro-sauropsidan or amphibian stem, — a theory which, with some modification, has received strong recent verification.

Professor Owen, who had held undisputed sway in England up to 1858, fought nobly for opinions which had been idolized in the first half-century, but was routed at every point. Huxley captured his last fortress when, in his famous essay of 1865, "Man's Place in Nature," he undermined Owen's teaching of the separate and distinct anatomical position of man. We can only appreciate Huxley's fighting-qualities when we see how strongly Owen was intrenched at the beginning of this long battle royal. He was director of the British Museum, and occupied other high posts; he had the strong moral support of the government and of the royal family, although these were weak allies in a scientific encounter.

Huxley's powers of rapid generalization of course betrayed him frequently. His *Bathybius* was a groundless and short-lived hypothesis; he went far astray upon the phylogeny of the horses. But these and other errors were far less attributable to defects in his reasoning powers than to the extraordinarily high pressure under which he worked for the twenty years between 1860 and 1880, when duties upon the Educational Board, upon the Government Fisheries Commission, and upon Parliamentary committees crowded upon him. He had at his command none of the resources of modern technique. He cut his own sections. I remember once seeing some of his microscopic sections. To one of our college junior students working with a Minot microtome Huxley's sections would have appeared like a translucent beefsteak, — another illustration that it is not always the section which reveals the natural law, but the man who looks at the section.

Huxley was not only a master in the search for truth, but in the way in which he presented it, both in writing and in speaking; and we are assured, largely as he was gifted by nature, his beautifully lucid and interesting style was partly the result of deliberate hard work. He was not born to it; some of his early essays are very labored. He acquired it. He was familiar with the best Greek literature, and restudied the language. He pored over Milton and Carlyle and Mill. He studied the fine old English of the Bible. He took as especial models Hume and Hobbes, until finally he wrote his mother tongue as no other Englishman wrote it. Take up any one of his essays, — biological, literary, philosophical; you at once see his central idea and his main purpose, although he never uses italics or spaced letters as many of our German masters do to relieve the obscurity of their sentences. We are carried along upon the broad current of his reasoning without being confused by his abundant side illustrations. He gleaned from the literature of all time until his mind was stocked with apt similes. Who but Huxley would have selected the title "Lay Sermons" for his first volume of addresses; or, in 1880, twenty-one years after Darwin's work appeared, would have entitled his essay upon the influence of this work, "The Coming of Age of the Origin of Species"? Or to whom else would it have occurred to repeat over the grave of Balfour the exquisitely appropriate lines: —

> "For Lycidas is dead, dead ere his prime,
> Young Lycidas, and hath not left his peer."

Who else could have inveighed thus against modern specialization: "We are in the case of Tarpeia, who opened the gates of the Roman citadel to the Sabines and was crushed by the weight of the reward bestowed upon her. It has become impossible for any man to keep pace with the progress of the whole of any important branch of science. It looks as if the scientific, like other revolutions, meant to devour its own children; as if the growth of science tended to overwhelm its votaries; as if the man of science of the future were condemned to diminish into a narrower specialist as time goes on. It appears to me that the only defence against this tendency to the degeneration of scientific workers lies in the organization and extension of scientific education in such a manner as to secure breadth of culture without superficiality."

What Haeckel did for evolution in Germany, Huxley did in England. As the earliest and most ardent supporter of Darwin and the theory of descent, it is remarkable that he never gave an unreserved support to the theory of natural selection as all-sufficient. Twenty-five years ago, with his usual penetration and prophetic insight, he showed that the problem of variation might, after all, be the greater problem; and only three years ago, in his "Romanes Lecture," he disappointed many of the disciples of Darwin by declaring that natural selection failed to explain the origin of our moral and ethical nature. Whether he was right or wrong we will not stop to discuss, but consider the still more remarkable conditions of Huxley's relations to the theory of evolution. As expositor, teacher, defender, he was the high priest of evolution. From the first, he saw the strong and weak points of the special Darwinian theory. He wrote upon the subject for thirty years, and yet he never contributed a single original or novel idea to it; in other words, Huxley added vastly to the demonstration, but never added to the sum of either theory or working hypothesis, and the contemporary history of the theory proper could be written without mentioning his name. This lack of speculation upon the factors of evolution was true throughout his whole life. In the voyage of the "Rattlesnake" he says he did not even think of the species problem. His last utterance regarding the causes of evolution appeared in one of the *Reviews* as a passing criticism of Weismann's finished philosophy, in which he implies that his own philosophy of the causes of evolution was as far off as ever; in other words, Huxley never fully made up his mind or committed himself to any causal theory of development.

Taking the nineteenth century at large, outside of our own circles of biology, Huxley's greatest and most permanent achievement was his victory for free thought. Personally we may not be agnostic; we may disagree with much that he has said and written, but we must admire Huxley's valiant services none the less. A reformer must be an extremist, and Huxley was often extreme, but he never said what he did not believe to be true. If it is easy for you and for me to say what we think in print and out of print now, it is because of the battles fought by such men as Huxley and Haeckel. When Huxley began his great crusade, the air was full of religious intolerants and, what is quite as bad, scientific shams. If Huxley had entered the contest carefully and guardedly, he would have been lost in the enemy's ranks; but he struck right and left with sledge-hammer blows, whether it was a high dignity of the Church or of the State. Just before the occasion of one of his greatest contests, that with Gladstone in the pages of the *Contemporary Review*, Huxley was in Switzerland completely broken down in health, and suffering from torpidity of the liver. Gladstone had written one of his characteristically brilliant articles upon the close correspondence between the Order of Creation as revealed in the first chapter of Genesis and the Order of Evolution as shown by modern biology. "When this article reached me," Huxley told me, "I read it through, and it made me so angry that I believe it must have acted upon my liver. At all events, when I finished my reply to Gladstone I felt better than I had for months past."

Huxley's last public appearance was at the meeting of the British Association at Oxford. He had been very urgently invited to attend, for exactly a quarter of a century before the Association had met at Oxford, and Huxley had had his famous encounter with Bishop Wilberforce. It was felt that the anniversary would be an historic one, and incomplete without his presence, and so it proved to be. Huxley's especial duty was to second the vote of thanks for the Marquis of Salisbury's address, — one of the invariable formalities of the opening meeting of the Association. The meeting proved to be the greatest one in the history of the Association. The Sheldonian theatre was packed with one of the most distinguished scientific audiences ever brought together, and the address of the Marquis was worthy of the occasion. The whole tenor of it was the unknown in science. Passing from the unsolved problems of astronomy, chemistry, and physics, he came to biology. With delicate irony he spoke of the "comforting word, evolution," and passing to the Weismannian controversy, implied that the diametrically opposed views so frequently expressed nowadays threw the whole process of evolution into doubt. It was only too evident that the Marquis himself found no comfort in evolution, and even entertained a suspicion as to its probability. It was well worth the whole journey to Oxford to watch Huxley during this portion of the address. In his red doctor-of-laws gown, placed upon his shoulders by the very body of men who had once referred to him as "a Mr. Huxley," he sank deeper into his chair upon the very front of the platform and restlessly tapped his foot. His situation was an unenviable one. He had to thank an ex-Prime Minister of England, and present Lord-Chancellor of Oxford University, for an address the sentiments of which were directly against those he himself had been maintaining for twenty-five years. He said afterward that when the proofs of the Marquis' address were put into his hands the day before, he realized that he had before him a most delicate and difficult task. Lord Kelvin (Sir William Thompson), one of the most distinguished living physicists, first moved the vote of thanks; but his reception was nothing to the tremendous applause which greeted Huxley in the heart of that university whose cardinal principles he had so long been opposing. Considerable anxiety had been felt by his friends lest his voice would fail to fill the theatre, for it had signally failed during his Romanes Lecture delivered in Oxford the year before; but when Huxley arose he reminded you of a venerable gladiator returning to the arena after years of absence. He raised his figure and his voice to its full height, and with one foot turned over the edge of the step, veiled an unmistakable and vigorous protest in the most gracious and dignified speech of thanks.

Throughout the subsequent special sessions of this meeting Huxley could not appear. He gave the impression of being aged but not infirm, and no one realized that he had spoken his last word as champion of the law of Evolution. He soon returned to Eastbourne. Early in the winter he contracted the grippe, which passed into pneumonia. He rallied once or twice, and his last effort to complete a reply to Balfour's "Foundations of Belief" hastened his death, which came upon June 29, at the age of seventy.

I have endeavored to show in how many ways Huxley was a model for us of the younger generation. In the central hall of the British Museum of Natural History sits in marble the life-size figure of Charles Darwin. Upon his right will soon be placed a beautiful statue of Richard Owen; and I know that there are many who will enjoy taking some share in the movement to complete this group with the noble figure of Thomas Henry Huxley.

FOURTH LECTURE.

PALÆONTOLOGY AS A MORPHOLOGICAL DISCIPLINE.

PROF. W. B. SCOTT.

(PRINCETON UNIVERSITY, PRINCETON, N.J.)

THE day has forever gone by when any one mind, however profound and comprehensive, can take all knowledge for its province. Increase of knowledge, like advance of civilization, necessarily brings with it a division of labor, and each of the great branches of science becomes more and more minutely divided and subdivided for the purposes of investigation. Such subdivision greatly enhances the efficiency of the individual worker, enabling him to concentrate his attention upon some definite problem of more or less limited scope, and, so far, it is advantageous. On the other hand, like most human devices, it has its drawbacks, and what is gained in one direction is apt to be lost in another. One great and growing evil is the subdivision of *knowledge* which accompanies specialization of research. The worker finds the greatest difficulty in keeping abreast of all that is being accomplished by fellow laborers in his own field; how, then, shall he find time to learn anything of the work in other fields? Not to do so involves the penalty of such a narrowness of view as will inevitably lessen the value of his own work, because deductions drawn legitimately enough from a single line of investigation often appear absurd when tested by a wider range of facts. Many a blunder might be avoided were the worker's vision not so strictly limited by the boundaries of his own speciality.

The narrowing effects of this subdivision of knowledge result in a more or less marked loss of sympathy and mutual understanding between the representatives of the different branches of the same science. To magnify one's own office is a very human infirmity, but it involves a minimizing of the offices of others. Science is not advanced by the sneers of its representatives at one another as mere "species-makers," or "section-cutters," or "closet-naturalists," as the case may be. One is prone to regard with instinctive distrust results which run counter to cherished convictions, or which ill harmonize with prevalent theories and call for a radical readjustment of opinion. Naturally, the investigator is apt to place undue reliance upon the methods with which he is familiar and to undervalue other ways of attacking the same problem. Evidence derived from other lines of investigation means less to him and is the more readily overlooked and ignored. Perhaps the greatest danger which at present threatens the healthy growth of zoölogical science in all its branches is the ever-increasing tendency to ambitious speculation, founded upon the narrowest basis of fact. So much of a theoretical taint attaches to nearly all morphological work, as to cause hesitation in fully accepting it, and one often feels in reading that we have gone back to the days of the transcendental anatomists. The glib use of phrases and formulæ, which hide ignorance under the guise of "explanations" which do not explain, is an outgrowth of the same tendency. It is the fashion to measure with elastic standards, which expand and contract to meet the needs of each case. Dogmatism and narrow-mindedness have ever been closely akin.

The obvious corrective for many of these evils is to take a wider view of our subject, and for each of us to learn something of the methods and results of workers in other fields than our own. I wish to invite your attention to a branch of morphology, the bearings of which are much misapprehended by the representatives of other departments of the same science, and which, where not completely ignored, is often wofully abused, namely, the subject of palæontology. This science has too long been abandoned to the geologist, but morphologists are coming to see that they have an interest in it, and sometimes condescend to make use of such parts of its data as favor their opinions.

Even yet, however, the necessary and close connection which obtains between palæontology and geology leads many to the assumption that its relation to morphology is, at best, very remote; but this assumption is quite unjustified, and proceeds from a confounding of the two quite distinct aspects and offices of palæontology. One of these offices is to determine the chronological succession of the rocks, and in this morphology is very indirectly concerned; but the other office is the study of fossils as organisms, and here Huxley's dictum thoroughly applies: "The only difference between a collection of fossils and one of recent animals is that one set has been dead somewhat longer than the other." This is a shining example of the "true word spoken in jest."

The great problems of morphology are the same for all workers in that science; it is the method of attacking them which differs. If I may be allowed to quote what I have elsewhere said, I would again call attention to the very instructive character of the analogies which exist between the history, aims, and methods of animal morphology and those of comparative philology. "In both sciences the attempt is made to trace the development of the modern from the ancient, to demonstrate the common origin of things now widely separated and differing in all apparent characteristics, and to establish the modes in which, and the factors or causes by which, this solution and differentiation have been effected. At the present time morphology is still far behind the science of language with regard to the solution of many of these kindred problems, and can hardly be said to have advanced beyond the stage which called forth Voltaire's famous sneer: "L'étymologie est une science où les voyelles ne font rien et les consonnes fort peu de chose." Of the animal pedigrees, now so frequently propounded, few have any better foundation than the guessing etymologies of the last century, and for exactly the same reason. Just as the old etymologists had no test to distinguish a true derivation from a false one, except a likeness in sound and meaning in the words compared, so the modern morphologist is yet without any sure test of the relationships of animals, except certain likenesses or unlikenesses of structure. How much weight is to be allowed a given similarity, and how far this is offset by a dissimilarity which accompanies it, we have, as yet, few means of determining, and have still to discover those laws of organic change which shall render the same service to morphology as Grimm's law has done to the study of the Aryan tongues."

Philology was raised to the dignity of a true science by the laborious tracing back of modern words, step by step, to their ancient origins through all their intermediate gradations, and sound principles of etymology could not be established until this was done. Morphology must profit by this lesson and must imitate the method of the science of language. Not until many long phylogenetic series have been recovered can the law of change be worked out. It is just here that palæontology is fitted to render invaluable services to the common cause.

As every one is aware, the principal methods of morphological inquiry are comparative anatomy, embryology, and palæontology, each of which has its great advantages, but accompanied by its own peculiar drawbacks and limitations. Lack of time will prevent any discussion of Bateson's proposed new method from the study of variation. I have elsewhere examined that at some length.

The foundation and corner-stone of the whole structure of morphology must ever be comparative anatomy, an accurate knowledge of which is indispensable to successful prosecution of the other departments of inquiry. This method has, in the hands of the masters, registered many great triumphs in the solution of difficult problems of homology, and of the mutual relationships of animal groups. At the present time, the tendency is to give more and more weight to its determinations. On the other hand, finality cannot be reached by this method. It suffers from the very significant drawback of possessing no sure criterion by which to distinguish between those similarities of structure which result from actual genetic relationship and those which are due to parallel or convergent development, and thus to determine the taxonomic value of a given likeness or unlikeness. It is an exceedingly common fallacy to assume that because a number of allied groups display a certain structure, their common ancestor must also have possessed it. This may have been the case, but it is almost as likely not to have been, because the structure in question may have been many times independently acquired. While the comparative method frequently enables us to discriminate between the two classes of phenomena, it generally does not do so, and it never can give entire certainty upon this point.

On comparing the humerus of the horses with that of the camels, we find in each a characteristic difference from other artiodactyls and perissodactyls and agreement with each other,—a feature which may be described in brief as the duplicity of the bicipital groove and presence of a bicipital tubercle. It is *a priori* probable that such an isolated resemblance between two widely separated groups is due to convergence, and yet the comparative method can give us no assurance that this is not a primitive ungulate character retained in these two series and lost in the others. Having recovered the various extinct genera of both these phyla, we may trace out the gradual transformation of the humerus and definitely show that the resemblance has been independently acquired at a comparatively late period and is not a case of a persistent primitive feature.

In short, the difficulty of reaching firmly fixed conclusions upon questions of homology and relationship by the exclusive use of comparative anatomy lies in the fact, that this method deals only with the modern assemblage of animals, a mere fragment of that which has existed in former times. It is like attempting to work out the etymology of a language which has no literature to register its changes.

The second method of morphological inquiry, embryology, has had a somewhat chequered career. Not many years ago it was universally regarded as the infallible test of morphological theory and the principle that the ontogeny repeated the phylogenetic history in abbreviated form was accepted, almost without question, as a fundamental law. But this view has fallen somewhat into discredit. The admission which very early had to be made, that "cenogenetic" features of development were imposed upon or substituted for those due to ancestral inheritance, opened the door to an unduly subjective way of dealing with embryological evidence and deprived the method of that authoritative character which had so generally been ascribed to it. Now the whole recapitulation theory is boldly called in question, and, in the admirable lecture delivered last year in this place, Prof. E. B. Wilson showed the untrustworthy nature of the embryological criterion of homology. The difficulty in this case lies in the absence of any "canons of interpretation" (to use Bateson's phrase) by which the contradictory data of embryology may be harmonized into a consistent whole. To take a concrete illustration : The ontogenetic development of the horse's teeth would give us a very inadequate and indeed false conception of the actual steps of change by which the modern type of dentition has been attained, nor would embryology show that the horse is descended from five-toed ancestors. Knowing, as we do from the fossils, the phyletic series, the embryological facts may be readily understood. It is an undue reliance upon such facts which has led to the concrescence theory of tooth development now so rife in Germany, and which seems so absurd when viewed in the light of palæontology.

I have no intention of belittling the splendid services which embryology has rendered to morphology, but merely to point out that this method alone cannot reach finality any better than comparative anatomy. It resembles dealing with a literature that has been vitiated by many forgeries, only the grossest and most palpable of which can be readily detected.

A third method of attacking morphological problems is that offered by palæontology. Let us begin our consideration of this method by frankly acknowledging its drawbacks and limitations. (1) In the first place there is the imperfection of the geological record. Palæontology does not profess and never can hope to reconstruct the whole history of life upon the earth, or even the greater part of that history; very many chapters are irretrievably lost, and others are so fragmentary that they teach us little or nothing. The great sedimentary deposits which contain nearly the whole recorded history of the globe were laid down under water, and for a land animal or plant to be entombed there is a lucky accident. If all we could learn of the terrestrial life of North America had to be deciphered from the fragments enclosed in the oceanic deposits along its shores, how very imperfect would our knowledge be! Although the estuarine, swamp, and lake formations, which occur on such a grand scale among the rocks of the earth's crust, have preserved whole chapters in the history of terrestrial life with wonderful fullness and accuracy, they are all too few and too widely separated to form any complete record. Even in a continuous series of marine deposits, representing vast periods of time, there are sure to be gaps of greater or less importance in the record. Changes in the depth of water and the character of the bottom will drive out one set of forms from that locality and bring in another, which has no genetic connection with the former, which may perhaps return with a renewal of the old conditions. Many groups of organisms are incapable of preservation in the fossil state, except under the rarest conditions — conditions which occur so seldom and so widely separated in space and time, as to render hopeless any attempt to reconstruct a continuous story from them.

The very circumstances under which organisms are preserved in the rocks offer another obstacle to the determination of phyletic series. On examining large collections of fossils from several successive horizons, we find that the majority of the species and even of the genera are confined to one or two formations, and that each succeeding fauna is recruited partly by migrations from other regions and partly by the rapid expansion of comparatively few adaptive and plastic types, while most of the forms which were especially well fitted for the older conditions die out under the new. The collections are, of course, largely made up from the abundant and dominant species of each horizon, which frequently are not the ancestors of those which will be dominant in the succeeding one. The sudden appearance, as it so often seems to be, of a fully differentiated group is sometimes due to that cause, sometimes to a migration from some other region. Even in phyletic series which are well-nigh complete, there is a tendency for each successive genus to undergo similar cycles of specific variation and this adds to the confusion, the very completeness of the record increasing the difficulty of its interpretation.

(2) A second drawback to the palæontological method of inquiry lies in the incomplete preservation of those organisms which are fossilized. Of plants we find, for the most part, only scattered leaves, rarely the reproductive organs, stems, or roots, and often the proper association of the various parts requires the strenuous labor of years. Of animals, except under exceedingly rare circumstances, only the hard parts, teeth, bones, shells, and the like, are preserved, and in the case of vertebrates how seldom is even the skeleton completely recovered! As in plants, the association of the various parts of a single skeleton may require the long-continued and laborious efforts of many workers. Extraordinary blunders have sometimes been committed in this work. In the remarkable genus *Chalicotherium* the skull was at first referred to one mammalian order and the feet to another, and Forsyth-Major's suggestion that they all belonged together was received with incredulity. Of the even more curious *Agriochœrus* the head was ascribed to one order, the fore-leg to a second, and the hind-foot to a third.

The utterly false notion, which nothing seems able to eradicate, that the palæontologist can readily restore an extinct type from a single bone or tooth, ought to receive its quietus from such examples, though of course it will not. It is equivalent to saying that we have nothing to learn from the fossils, and that all possible types of structure are exemplified in the living world.

On account of this incompleteness of preservation we cannot learn much that we wish to know of the structure of extinct organisms. The nervous, vascular, muscular, and alimentary systems are entirely lost and can be inferred only from indirect and often insufficient evidence. Were the pearly nautilus extinct, our notions of the anatomy of the tetrabranchiate cephalopods would be very much astray, and in the cases of several groups of fossils we are quite unable to interpret the structure from what remains.

(3) A third difficulty in the way of a truly morphological

palæontology consists in the uncertainties of geological correlation, by which the relative age of formations in widely separated areas and different continents is to be determined. It may and often does make a vital difference in the construction of a phylogeny, whether a given set of rocks in North America is older or younger than one in Europe, with which it is correlated. The principles according to which such correlation is to be made are still somewhat indeterminate, and not a few geologists maintain that the problem is an insoluble one. On the other hand, it is essential to the palæontologist that it should be solved, and already a very encouraging beginning has been made.

(4) In the fourth place the apparent order of succession of organisms in the stratified rocks must not be too implicitly and uncritically accepted. Animals and plants diffuse themselves as widely as possible until stopped by some impassable barrier. During the long ages of the world's history these migrations have ever been in progress, and they greatly confuse the record when we attempt to read it in terms of evolutionary descent. A species in a newer formation, which appears to be derived from one in an older horizon of the same region, may, as a matter of fact, have had an entirely different ancestry and have migrated half around the globe to the place where it occurs. To make these distinctions theoretically is easy, to apply them very difficult.

(5) Lastly should be mentioned a practical drawback to the palæontological method, namely, its costliness. The naturalist may find much to do in other departments at small expense, which will be a source of infinite pleasure to himself and of great value to science. Every field and wood, every pond and stream, and above all the sea, offer boundless stores of material. Even the side of palæontology which bears upon stratigraphy and historical geology may be taken up to great advantage by the private worker who happens to live in a favorable locality. With palæontology as a branch of morphology, however, the case is unhappily very different. Here great collections brought together without much regard to cost, skilled workers to prepare the specimens, and great

buildings in which to house them are indispensable. Distant regions must be examined and the whole world ransacked for material. Many problems connected with the North American fauna must await their explanation until Asia can be thoroughly explored, while Africa and South America have already shown what a complete geological knowledge of those continents may be expected to teach. In this country the arid parts of the West have yielded a marvelous store of wonderfully preserved fossils, but great sums have been expended in gathering them, — an opportunity which falls to the lot of but few. It is to be hoped that the multiplication of museums may ere long put within the reach of all biological students something of these marvelous stores of wealth.

It might well seem that all these limitations and drawbacks would necessarily disqualify palæontology as a morphological subject from being of the smallest real importance, but such a conclusion would be highly erroneous. Several of the limitations are but partial, not applying to particular cases, while others are difficulties that further investigation may hope to remove, not insurmountable obstacles. Every year new forms are discovered and better material of known forms. Though the White River Bad Lands have for more than half a century been classic collecting ground, hardly a season passes that several new genera are not registered from there, and, better still, types before known only from fragments are gradually made more and more complete. From the middle Eocene to the lower Miocene there is in the West an almost unbroken transition which is bringing forth a truly magnificent series of evolutionary stages.

While palæontology, as we have seen, does not profess to give an unbroken life-history of the earth, yet it has certain preëminent advantages which neither comparative anatomy nor embryology possesses, and which fit it to form an invaluable supplement to those other methods of morphological investigation.

(1) In the first place, it gives us in many cases actual phyletic series in their true order of succession in time. In many groups of animals we have already recovered phyletic

series so full, so complete, that no observer can hesitate to accept them as representing actually or very nearly the successive steps of evolutionary change in the order in which they occurred. Little confidence may, perhaps, be placed in these phyla by those who have not made a special study of them, and it may be imagined that fuller knowledge will require them to be completely changed. But when we find such a series as that of the horses, leading back by almost imperceptible gradations from the great monodactyl living forms to their little five-toed progenitors in the far distant Eocene times, doubt becomes well-nigh impossible. A limit of error is placed by the stratigraphical order, the geological and morphological successions coinciding beautifully. Whatever changes in the details of such a series, a radical reconstruction of it is not in the least likely to be called for. Few observers, if any, would now uphold the arrangement of the equine phylum proposed by Kowalevsky, namely, *Palæotherium*, *Anchitherium*, *Hipparion*, *Equus;* and yet it is surprising to see how the general character of this series and the deductions as to the manner of evolution which may be drawn from it agree with those made on the basis of the equine series as we now have it. Kowalevsky's mistake merely consisted in putting certain members of the side branches into the main line of descent, and that similar errors have been made in accepted phylogenies is not at all unlikely. The correction of such errors will, however, change the general result but little, and we may appeal with considerable confidence to the conclusion which legitimately follows from a study of these phylogenies.

Fortunately, the well-defined phyletic series which have already been made out occur in very widely separated animal groups, — mammals, reptiles, cephalopods, brachiopods, echinoderms, etc., — so that the points in which they agree are apt to prove of general application and validity. The cephalopods are particularly valuable in this connection, because in them the embryonic and young stages of the shell are preserved in the adult, and thus conclusions have a distinct support from embryological considerations. To recur to the linguistic analogy, we have here at least fragments, and sometimes very extensive ones, of the various literatures which register the changes of language, and in the original documents which bear evidence of their dates and succession, and which, however incomplete, have not been falsified by forgeries and late interpolations. In this way we may establish unequivocally some, at least, of the animal pedigrees, which it is one of the great objects of morphology to construct, and thus to correct the results obtained by the other methods of inquiry. Palæontology further enables us accurately to discriminate between resemblances which are due to genetic affinity and those which result from parallelism or convergence.

To illustrate: On grounds of comparative anatomy Flower classified the land Carnivora into three sections: the Cynoidea, or dogs; the Arctoidea, containing the bears, raccoons, and mustelines; and the Aeluroidea, including the civets, hyenas, and cats. This classification has found wide favor and very general acceptance, but palæontology shows it to be untenable. The extinct phyla show that the dogs and bears are very closely akin, as are the mustelines, civets, and hyenas, while the cats occupy a very isolated position, and are not closely allied to any of the other families. The anatomical characters which suggested Flower's system are in part examples of convergence and in part due to the retention of primitive characters in some groups and their loss in others.

Again, reasoning from embryological data, Röse and others have propounded the theory that the complex, multicuspidate, mammalian tooth has been formed by the coalescence of many simple teeth. The phyletic series enable us to follow the evolution of these teeth step by step, and demonstrate the incorrectness of the "concrescence theory." In fact, the great lesson which the study of the phyla continually brings home to the observer is, that trustworthy results are to be obtained only by the laborious and minute tracing of the changes through every step of the way. Fragmentary series are not to be depended upon, and the wider the gaps between their members the more uncertain is their connection.

(2) The reconstruction of pedigrees, the solving of homol-

ogies, the determination of relationships, and the establishing of classification upon a sound and natural basis, important as these are, are yet only a part of the great task which morphology has set before itself. We wish to penetrate more deeply into the mystery of nature, and learn how and why these changes have occurred; or, in other words, to discover the manner in which, and the efficient causes by which, development is effected. On these subjects there is, as yet, wide divergence of view among morphologists. The postulates and assumptions upon which morphological discussions are founded are, in great measure, incapable of proof, and appeal with very different degrees of force to different minds. Modes of development which appear axiomatic to one observer are by another regarded as absurd. All are agreed that there are limits to the possibilities of change; no one attempts to derive a butterfly from a beetle, or a horse from a cow; but just how and where these limits should be drawn it is at present impossible to say. It is this uncertainty which refers the question to the individual judgment, and leaves the way open for such radical differences of opinion.

To the solution of these problems of evolutionary modes palæontology offers most valuable assistance, drawn from the study of actual phyla. It might seem that this was merely arguing in a circle, because the construction of phylogenetic series involves certain presuppositions as to what changes are and what are not possible, and we then proceed to prove the presuppositions by the phyla thus constructed. But the cautious, step-by-step method, guarded by the order of appearance in time, offers a way of escape, and enables us to construct phyla in harmonious structural and stratigraphical succession, which must very nearly represent the actual stages of change. Only a beginning has been made in this work, but the results drawn from an examination of widely separated phyla, such as mammals, gasteropods, and cephalopods, are so consistent and harmonious as to be full of promise for the future.

Limitations of time and space forbid an attempt to fully consider here all the deductions which have been suggested and rendered more or less probable by this method, but one or two principles which stand out with especial clearness may be mentioned.

(*a*) Evolution is ordinarily a continuous process of change by means of small gradations. The continuous character of a phylum is apt to be proportional to the relative abundance of its representatives in the strata, which is equivalent to saying that well-known series are continuous, while apparently discontinuous series are imperfectly known. This does not imply that the rate of change was always uniform, — it probably was not, — or that a sudden alteration of conditions may not bring about discontinuity, or *per saltum* development. It means that the usual and normal mode of advance is by continuity of change.

(*b*) Development is, in most instances, direct and unswerving. The rise of new forms, and the decadence and degeneration of old ones, are not ordinarily by zigzag and meandering paths, but by relatively straight ones; and though, of course, a path once taken may be diverged from, yet in such a case it is not regained. This applies particularly to the organism as a whole; in minor details more latitude is permissible. The evidence is not yet sufficient to show just how widely applicable this principle is.

(*c*) Parallelism and convergence of development are much more general and important modes of evolution than is commonly supposed. By parallelism is meant the independent acquisition of similar structure in forms which are themselves nearly related, and by convergence such acquisition in forms which are not closely related, and thus in one or more respects come to be more nearly alike than were their ancestors. While some observers have tacitly or explicitly denied the reality of these processes, most authorities have been compelled to admit them. What palæontology has done, and is doing, is to show the universality of these modes of development, and to point them out in directions where they had not been suspected. To give a few examples. The crescentic, or selenodont molar, has been separately acquired by no less than three groups of artiodactyls, and probably others as well. The spout-shaped odontoid process of the axis has independently developed in the horses, the tapirs, and in three artiodactyl series. The true ruminants (Pecora) of the present day are, among other characteristics, distinguished from the remaining artiodactyls by the hollow tympanic bullæ, which in the pigs, tragulines, and camels are filled with cancelli, or spongy bone. In Oligocene times only the camels had acquired the cancelli; the other groups, though already differentiated as such, still had hollow and inflated tympanics. Lists of such parallelisms in single characters might be multiplied almost indefinitely, but they also occur in whole groups of structures. The camels have in teeth, skull, vertebræ, and limbs many points of resemblance to the true ruminants, which demonstrably are not due to inheritance from a common ancestor. The two great series of ungulates, the artiodactyls and perissodactyls, which are usually grouped together as the Ungulata *par excellence,* are examples of parallel development on a grand scale, their many resemblances being, for the most part, independently acquired. The flesh-eaters known as Carnivora include at least two, and probably three lines, which have been separately given off from the primitive flesh-eaters, or creodonts.

Such a mode of development greatly increases the difficulty of determining phylogenies, which would be very much easier could every notable resemblance at once be accepted as proof of relationship. It often renders impossible the proper classification of some isolated genus which seems to have several incompatible affinities. It emphasizes the necessity of founding schemes of classification upon the totality of structure, and of determining the value of characteristics, whether they are primitive or acquired, divergent, parallel, or convergent, before attempting to assign them their proper taxonomic value.

We may find a practical identity in teeth, skull, or feet as the outcome of these processes, but as yet no case is known where all these structures have become alike through the operation of either parallel or convergent development. Among the invertebrates the case is different. Hyatt has shown that the degenerate, straight-shelled, ammonoid genus *Baculites* is a polyphyletic group, and derived from several distinct stocks, both European and American. Würtenberger points out that the so-called *Ammonites mutabilis* is not a true species, but a composite group, made up by the convergence of several distinct lines to a common. This case is peculiarly significant, because it would hardly have been detected had not the embryonic and young stages of the shells been preserved.

It seems the most obvious of commonplaces to say that numerous and close resemblances of structure are *prima facie* evidences of relationship. Yet the statement is true, even though the resemblances have been independently acquired, because parallelism is a more frequently observed phenomenon than convergence, and because the more nearly related any two organisms are, the more likely are they to undergo similar modifications.

All this brings us back to the thesis so frequently insisted upon already, that the only safe and trustworthy method of constructing phylogenies is by tracing the development, step by step, through all its gradations; and until this is done the classification of any group can be but tentative and provisional, that is, if we intend classification to express relationship.

No department of biological science is at present the scene of such vigorous controversy as that which deals with the factors of evolution, the causes which determine the development of new forms, and the problems of heredity which are inseparably connected with them. Palæontological evidence will prove to be of much importance in this connection also, but it cannot well have more than a corroborative value. Though the examination of long and complete phyla brings to light much that is suggestive concerning the factors which have brought these changes to pass, and any rational theory must embrace and explain these facts, yet the deciding weight must probably come through the physiological and experimental method. Time fails to deal with such far-reaching questions here, and yet it may be well to call attention to the necessity of avoiding a dogmatic and intolerant attitude, and to deprecate any premature attempt to exclude this or that class of factors from consideration. In most of the recent writings upon the efficient causes of evolution you will find expressed or implied the feeling that these matters are not so simple and intelligible as we once supposed, and that we are yet only upon the threshold of its solution. The study of palæontology will not tend to dispel this feeling of mystery.

Another department of biological science in which palæontology has proved of great value, and will become more and more so in the future, is that which deals with the geographical distribution and migrations of organisms. Though not a branch of morphology, this subject has a very significant bearing upon that science, and cannot be ignored in any comprehensive theory of evolution. This, again, is too large a field to enter upon at the close of a lecture. It must suffice, therefore, to hint at the many cases in the existing distribution of animals, which seem so puzzling and capricious, and which are so readily explained by a study of the past. That the nearest allies of the South American llamas should be the camels of the Old World seems unaccountable until we learn that North America was the original home of the entire tribe. The occurrence of the tapirs in South America and in the Malay Peninsula becomes intelligible enough when we learn that this genus is of very high antiquity, and was formerly represented in every part of the northern hemisphere.

The more fully the past is recovered the more completely the former land connections of the various continents are made out, the more comprehensible do the seeming anomalies of the present order of things become, — a proposition which applies to more than problems of geographical distribution.

The foregoing consideration of palæontology as a branch of morphological science is necessarily brief and very inadequate, but it will suffice, I trust, to show that its claims upon the attention of morphologists should not be ignored, and that it is admirably fitted to throw light upon many obscure problems. In conclusion, let me point out that final and lasting results are not to be gained by an exclusive adherence to any method of morphological inquiry, but by a combination of all of them. Each is able to supplement the others, and it is folly to reject such aid. Already most encouraging results have followed from this combined method of work, and it is devoutly to be wished that its scope may be more and more extended. As an example may be cited the recent investigations upon the mammalian dentition. From palæontological phyla we have learned to distinguish the homologies of the cusps, and the way in which a complex tooth is gradually formed from a simple one. Embryology, on the other hand, has shown the relations of the successive dentitions to one another in a fashion that palæontology could by no possibility accomplish unaided. As another example may be mentioned Wincza's discovery of a bony clavicle in the embryo of the sheep, which was soon followed by the still more unexpected one of vestigial bony clavicles in certain extinct artiodactyls, confirming and explaining the first. Embryology has taught us that the large element in the carpus of the Carnivora known as the scapho-lunar was formed by the coalescence of three separate bones, — the scaphoid, lunar, and centrale. Later the fossils were unearthed, which showed that the embryonic and transitory condition of the modern forms was the permanent and adult structure of the primitive Eocene flesh-eaters.

The more the combined method is employed the more fruitful does it appear. Nor should the combination be restricted to the technically morphological subjects. Experimental embryology has already won some notable triumphs, and that is a physiological quite as much as a morphological province.

In the ever-increasing complexity of modern civilization a more and more important rôle is played by systematic coöperation, specialists combining for joint work which neither could accomplish alone. Is it Utopian to wish that some such organized scheme of attack upon biological problems shall be devised, when, instead of every man doing merely that which is right in his own eyes, we shall combine in a definite, orderly way to investigate a given topic in all its bearings? It may well be doubted whether any naturalist, however great his genius, will ever again be able to take such an exhaustive survey of biological data as Darwin did in his time. The enormous mass of accumulated facts already far transcends the power of any one mind to grasp, and it would seem that organized coöperation is the only method of dealing with such vast accumulations. When that time arrives the palæontologist will be able to render even more conspicuously valuable services than he has done in the past.

FIFTH LECTURE.

EXPLANATIONS, OR HOW PHENOMENA ARE INTERPRETED.

BY A. E. DOLBEAR.

(TUFTS COLLEGE, COLLEGE HILL, MASS.)

How long a time mankind has been on the earth no one knows. When I was a lad I was taught that the earth was made about six thousand years ago. Archbishop Usher's chronology was accepted by all except a few geologists, and their conclusions were considered as speculative vagaries, invented by men whose object was to bring the Bible into disrepute, and against whom it was the duty of men who loved the truth and who believed they possessed it to warn the young. Now it is believed that the great pyramid of Gizeh has been standing for nearly, if not quite as long a time, and Egypt was a thickly settled country with well-established government, laws, customs, religion which had then existed for a long time. Back of Egypt was Assyria and other peoples, and farther back still other peoples, and so on till all was lost in an antiquity reaching back probably fifty thousand years and perhaps twice that period. What has brought about the change in opinion as to a matter of that character which cannot be rigorously demonstrated, and why has any one more than a speculative interest in it? The answer to the first is that new data have been found bearing upon the question which our ancestors did not have, and a necessity was felt for making every kind of testimony logically consistent with every other kind. To the second, one must say that every thoughtful person who is interested in his own existence and humanity has hopes and fears; he is aware without reasoning upon it that a knowledge of the past must help to a knowledge of the future, and if he can properly interpret the past of mankind he will the better know what to anticipate for them and himself. So long as creation was supposed to be by fiat and the universe to have sprung into existence just as Minerva was said to have sprung from the brain of Jupiter, there was no trouble. Everything was satisfactorily explained by saying God did it. The question how did not concern any one, for miracle was the method of deity, and needed no antecedent but the will of the deity. All effort was given to establishing the authenticity of the biblical record. It was held to be such an important matter that no one was allowed to question it, or assume even for an instant that it was not the exact truth. The importance of a knowledge of the past history of mankind is as great as ever; its interest has not abated but increased. The origin and destiny of mankind are still the primal questions, and all knowledge in any department of human effort has its main reason for the light it may throw on these.

In this, as in most other works, there are two ways which men have adopted to satisfy their philosophical wants. One is to assume what is thought to be an adequate fundamental cause or principle, a mode of operation, and a certain logical process also believed to be reliable, and with these to construct by a deductive process the observed phenomena. For instance, to account for, say, the Solar system as it appears to-day. Such a philosopher would assume first, the existence of a deity with the attributes of omniscience, omnipotence and will, existing and related to time and space as we are. Secondly, he assumes that the mode of operation was radically different from any he knows of or can imagine, namely, the creation of both matter with all its qualities and also energy as we know it, for we know of energy only as existing in something already formed. And thirdly, he assumes with these that he may trust his logical process and reach the conclusion that the existence of the Solar system and everything happening in it is properly explained by assumptions, neither of which are in accordance with human experience. For first, has not the proof, absolute proof, of the existence of God been the attempt and the despair of philosophers? If we possess it to-day in the sense that we possess proof, — say, of the North Pole or the existence of the ether of space, — where is it to be found? Proof of the latter compels assent as soon as perceived, yet every one feels there is something desirable lacking in the former. It may be more or less probable, but certainty is what we are talking about.

Again, creation implies a process by which nothing becomes something. If the matter which constitutes the world was simply formed out of something else which was not matter, then it is that something else we are concerned about, and the inquiry properly belongs to that antecedent something. Now all of our experiences in any field are with matter and with forms of energy. Experience with the former has led to the conviction that its quantity is not changed in the slightest degree by any kind of a physical or chemical process. Once it was thought possible to change lead to gold, but it was in the prescientific age when chemical products were not weighed in the balance, and the spectra of the elements had not been seen. Experience with energy has led to the formulation embodied in the doctrine of the Conservation of Energy, namely, that the quantity of energy in the universe is constant. No kind of changes alters the quantity. If these deductions from experience be true, it follows that either what we call matter and energy have always existed, or, if either had a beginning, it must have been by some process out of all relation to everything we know, — one which can neither be described nor imagined, and explanation is therefore impossible, if explanation means what we mean by it when applied to such a process as, say, the generation of electricity in a dynamo; for in this we have definite known antecedents of steam power, heat, and so on. In experience we have only transformations, all of which imply matter as the condition of transformations. The creation of energy is a radically different affair, and it is a fair question, by what warrant does any one assume a process wholly foreign to experience as a basis of a philosophy of experience?

Again, the fallibility of human logic has been so many times shown, and in so many different fields when applied in cases where verification has been possible, that one may well hesitate about holding very fast to any conclusion which has not yet been adjudicated by experience. This holds as true for what we call philosophy as for science. We are in possession of a body of scientific doctrines or propositions about material phenomena which are satisfactory to this extent : they have met all the criticism to which they have been subject by men of every nation who have concerned themselves with them. Such, for instance, are the doctrines of mathematics, of astronomy, of geology, and some others in physical science, all of which deal with verifiable matters, that is, with matter and the forms of energy and their relations. In gaining this degree of certainty there has been a series of steps taken tentatively, engrossing the attention of men interested in science for a century or two. The thing to note here is, that obvious as many of these propositions are to us, now they are pointed out, they were so far from obvious to our predecessors that almost every other conjecture was entertained, and often with no attempt at verification before the present ones were adopted. This is of so much importance that some examples may be useful to make plain the meaning. Take the case of the explanation of the position and motions of the earth, and other bodies. First, as to the center of creation about which sun, moon, and stars revolved. The apparent was taken to be the truth, and the difficulties of such an explanation of the apparent were quite ignored, and the necessity of having some sort of an answer to the question as to the causes of day and night was so great that such an explanation was thought to be better than nothing. After that came Ptolemy's explanation, a wonderful and intricate system of cycles and epicycles which mechanically would not work, but served for a time better than the one it displaced. Then came Copernicus with the plan of the sun as the center with the planets and the earth revolving about it. This simplified the problem, but the reason given for supposing the orbits of the earth and the planets to be circular was not a physical reason, — that is, not an observed or calculated one, but a metaphysical reason ; that is, one which was imagined to be in accordance with moral quality. The Almighty had made things perfect; a circle was the only perfect circuit. Kepler discovered that none of the bodies involved moved in circles but in ellipses, and this is known as one of Kepler's laws. But Kepler, unable to imagine how such bodies could move in such ellipses as he observed they did, and, like others, feeling obliged to give some sort of an explanation for the apparent anomaly, invented guiding spirits whose office was to thus move the heavenly bodies. Then came Sir Isaac Newton, who showed that, with gravitation assumed, all the observed motions were accounted for, and further, that the so-called perfect circle orbit was the only unstable orbit.

In this series of steps towards the explanation of observed phenomena, the first was wrong in every particular. The others were wrong, and wholly wrong, to just the extent they departed from simple mechanical relations and incorporated unmechanical and unrelated notions with their explanations. Again, it has been thought a reasonable explanation of the relations and motions of the bodies which make up the Solar system that they were thus created, each one at its proper distance from the sun, and with rotations and revolutions properly adjusted for stability. The Solar system started thus. No reason or explanation was needed save that it was the will of an omnipotent creator which, as already pointed out, is not an explanation but a reference to the unexplainable. Kant perceived that the involved relations were probably of a mathematical sort, and inferred there was probably some simple mechanical explanation of the whole arrangement. Laplace attacked the problem and showed if the material which now makes up the Solar system had been scattered in space in a gaseous form, gravitation would bring it to just such a system of globes, with masses, distances, rates of rotation and satellites as we find them to have. The telescopes at that time showed many patches of nebulous masses in the sky; but as the telescope was improved many of these patches were seen to be dense clusters of stars, and the inference was fairly allowable that with sufficient telescopic power all might in a similar way be resolved. The spectroscope, an instrument for determining whether matter is solid or gaseous, when turned towards the sky showed that there were vast numbers of gaseous masses there and in many degrees of condensation. This discovery was held to corroborate the idea of Kant and Laplace, so that to-day there is no astronomer who does not hold the view that the Solar system as we see it to-day is a growth, that it was not made as it is, and that gravity with the simple laws of motion are sufficient in themselves to organize the Solar system as we find it, and an explanation of it is an exposition of how these factors brought it about.

The distribution of land and water, mountains, valleys, rocks and their contents in like manner were held to be explained by the statement that they were thus created substantially as we find them. When it was noted that animal and vegetable remains were to be found in abundance in many rocks, very little thought was needed to induce the question: If these rocks have been in place from the beginning, how came they to be filled with evidences of marine life such as fossils attest? Did the ocean once cover the mountain tops? Once the attempt was made to explain their presence by reference to Noah's flood which was held to have covered mountain tops, but the fossils were to be found through great rock formations and through rock depths of miles. It was noticed presently that the lower formations had simpler forms and the lowest rocks none at all. There was but one meaning to all this, namely, the surface of the earth had been depressed and elevated above their present level, that the ocean must have once covered what is now a mountain chain. It was also noted that slow changes in elevation are now going on in many places. The coast of France is sinking, the coast of Norway rising. The temple of Jupiter Serapis has twice been submerged in the Mediterranean Sea and is now out of water. The Mississippi River is building shores in the Gulf of Mexico at the rate of a mile or two a year with the detritus brought from the central valleys of the United States, and Niagara Falls is retreating at the rate of a foot or two a year. Such phenomena imply unstable land and water surfaces. The physical features of the earth are changing slowly. In time they can change to an unlimited extent. Geologists explain all geologic phenomena as due to physical causes such as are now going on; but the implication is that, given simply time, everything we observe of this character is easily understood, — with no appeal to other than such factors as are at work before our eyes, — and, with such a background as is afforded by an appeal to astronomy, there is good reason for holding that no other physical factors than the ordinary type have been involved in the geologic phenomena. Geological facts are explained by presenting their physical antecedents, and the explanation stops when traced to these, that is to say, when in the territory of astronomy or physics.

Once more: only a generation ago men believed that all species of animals and plants upon the earth were descended from similar forms without modification from the original ones created by fiat. The horse of to-day is like his ancestor of thousands of years ago, the lily like the original. In like manner all plants and animals and men represented in form and qualities their prototypes. Not because any one had ever been a witness to such a process of creation nor because there were other evidences which deserved attention, but it was a kind of habit of mind to pretend to explain phenomena by referring to some inexplicable process out of all relations with experience. In 1846 a book was published anonymously, called *Vestiges of Creation*. It attempted to show that all the present forms of life might have resulted from the simplest forms of life by a series of small, almost insensible changes in the organisms, if these were continued for a great number of generations. The idea was condemned by almost everybody interested in the question, not from defective evidence, but simply because it required the abandonment of a belief that had not a particle of evidence in its favor. That is to say, an attempted explanation which had much experience in its favor was rejected by theologians and naturalists alike, and another explanation, having not a particle of evidence and no degree of probability, was held to. Since the time of Darwin all that has been changed. The view advocated in *Vestiges*, though not with such conclusiveness as by Darwin, has been generally adopted by naturalists of every nation.

To accept Darwin is to accept the proposition that there never was a first horse or first rose or first man. The ancestry of the horse has been traced back through a long series of forms as far as an extinct animal, known in zoölogy as the paleotherium, which was no more like a modern horse than is a tapir; but this distant animal may have been extinct for a million years or more. No matter how long now, the point is that the old notion has been given up, and appeal has been made for all changes in form, size, habits, and adaptations to processes now going on, and all appeal to other or superphysical agencies has been abandoned by naturalists of every country. This means that in such important matters as the phenomena of living things there is felt to be no necessity for going beyond ordinary factors operating to-day, in precisely the same sense as was the case of geology and astronomy. The explanations accord with experience, and exposition is only the presenting of factors and conditions in their proper order. The explanations in each of these are adequate only when the antecedents are sufficiently well known to make it plain they need no supplementary, unrelated factors.

We hear in these days of the forces of nature, of heat, of light, of electricity, and the latter especially is popularly considered as a very mysterious something which nobody can understand. These factors are supposed to act upon matter and compel it to do this or that, go here and there. Heat in the old books was often called caloric, and that was supposed to be an imponderable something which could now be in matter and now out. When in it, it caused the matter to exhibit certain kinds of phenomena; when it was out, none inquired as to where it was or what it was about. During this century it has been conclusively proved that heat is but a particular kind of motion. When one body strikes another body it imparts some of its motion to it for mechanical reasons, and if a body possessing heat motion comes in contact with another body having less of that kind, it imparts some of that heat to it. What one loses the other gains. There has been nothing more mysterious than an exchange of motion; there is no imponderable substance to be now in and now out, — only a change in the conditions. Taking this view of heat it is easy to see that the terminology served to mislead thinking; but the view here presented shows that heat cannot be properly called a force any more than the vibrations of a bell or a piano string can be called a force, and so heat is out of the category of force.

Light was also an imponderable substance. Now we know it to be wave motion in the ether, and the vibrations that constitute the heat of molecules set up these waves in the ether, and the latter conducts them away at the high rate of 186,000 miles a second. The heat motions are the antecedents of the light motions in the ether in every case, and every ray of light when traced back to its source ends in a vibrating molecule. So if heat be not a force, neither can light be so considered, and two of the imponderables are gone as forces.

Electricity as another wonderful force is known to originate in the motions of molecules, for both by chemical action and by heat action it is produced. It also disappears when allowed to do either chemical, thermal, or mechanical work. As it has molecular motion for its antecedent and molecular work for its resultant, it follows that its nature cannot be materially different from that of the others. Indeed, so well established are these interrelations between heat and electricity that large industrial enterprises are founded upon them. The point here is that electricity, as an independent something, — a force that may be summoned like an Afrite in *The Arabian Nights* to do duty for a while and then be dismissed from service to be no one knows where, — is an idea wholly wrong. It is a condition, not a thing, for electrical energy may be wholly transformed into heat energy or into light or other kinds of work. So far we have only matter and forms of motion in matter, and forces as such have no existence. And if this be true it will be well to abandon the notion of either of these agencies as forces or things having an existence apart from matter. There is no evidence for such a view, and any quantity of evidence against it. The explanation of the phenomena due to either or all of them requires nothing beyond the factors I have already named, and there is no need of assuming anything more mysterious than these. If all phenomena in the realm of the so-called inorganic nature be due to matter and its various motions,—and of this there seems to be little reason to doubt, and no one argues otherwise, — then what is the use of talking about forces of any kind, seeing they have no existence. How much difference this will presently make in one's conceptions any one may discover by omitting the use of the word "force" from his vocabulary for a day or two, whenever he discourses and attempts an explanation of a phenomenon. It will be perceived that the word is used generally as a pretentious substitute for ignorance.

Living things, both plants and animals, were thought for a long time to be endowed with a quality radically different from inanimate things. The processes of digestion, assimilation, growth, and the like were believed to be dependent upon a peculiar agency capable of dominating the ordinary chemical activities which otherwise would destroy the organism. This was called vital force. Organic chemistry was the name given to the processes by which a host of complex compounds were formed in living things, and vital force was credited with being the agency in all of them. By and by a chemist succeeded in producing in an artificial way a single one of these products, and the announcement was a stunner to both physiologists and chemists. Soon other chemists found artificial ways of making others, and to-day so great a number have been produced in the laboratory that chemists do not hesitate to express their belief that every organic substance, even protoplasm, may thus be formed, and that also in the animal body there is no such agency at all as was called vital force. Physiologists trace physiological phenomena without exception to the activities of ordinary forms of energy known as physical and chemical, not because chemists have been able to build up all compounds known, but because among the tens of thousands which have been thus formed there is nothing more required than what can be provided in a test tube; and also because it has been fairly well proved that there is a direct and quantitative relation between the energy of food and bodily activity of every kind; that no more comes out of the bodily machine in the shape of work, physical or mental, than is physically provided by the foods digested. So vital force as an agency in living things is as mythical as the other forces I have described as non-existent. An explanation, then, of the phenomena of life as manifested in either plant or animal is complete when the physical and chemical antecedents have been presented in their order and quantitative relations. There appears to be no reason for holding to the view that there is anything more mysterious or different in kind in so-called vital phenomena than there is in what goes on in a test tube in a physical laboratory. There may be a difference in complexity, not in agencies.

Of course everybody knows of what is called the conservation of energy which implies, as I have said already, that the quantity of energy in the universe is constant, and when any given kind appears, it is always at the expense of some other kind which has disappeared, and the two are equal. If the quantity of matter is not variable, — and that is precisely what all experience affirms, — and if the quantity of energy is also not variable, though its forms may be, then the apparent logic of the case is that one of the factors of energy must be the variable, and in fact energy as we know it is always *a product*. It does not exist as an entity. One cannot assume that the energy of a moving rifle bullet can be detached from it, so as to enable one to hold the bullet in one hand and the energy in the other. The variable factor is simply the rate of motion the bullet may have, and this rate of motion, whatever it may be in a given case, had its antecedent in some other body which lost the motion which was imparted to the bullet. If this be applied in every case, then it seems that every kind of phenomenon involving physical energy — and every phenomenon does involve such energy — must be due to changes in the kind and direction and amount of motions a body may have; and there is no reason for imagining or supposing in any given case the existence or activity of any agency differing from or related to those forms of energy which are investigated in physical science. Forces dethroned, and matter indestructible,—that is the result of the scientific activity of the past half century.

When one contemplates that proposition, and thinks of the wonderful variety of phenomena in the earth and in the heavens, and then attempts to realize even in a faint way how all this can possibly come about through the sole agency of motions of any kind, however complex in their combinations, he cannot but feel there must somehow and somewhere be an undetected slip in the logic, or there must be a factor, and a most important factor, left out; for at some time in the history of things, at any rate on the earth, there have appeared not only living things as plants and animals, but activities of another class, feelings and intelligence. Along with physical happenings and physical things there has come the senses and the intellect, the possibility of pleasure, the consciousness and delight in existence, hopes and fears, and other phenomena, which cannot by any jugglery of idea or language be resolved into molecular vibrations or rotations, or any other motions whatever. They are the things we live for, and care to live for. These qualities we find in experience to be always associated with matter and various forms of energy; but the character of the two classes of phenomena appears so different as to have led philosophers to the conclusion that they could exist apart, having no necessary relation to each other; indeed, the terms "matter" and "mind" are generally set against each other as contrasting things which have nothing in common. Matter has been called dead, inert, and incapable of doing anything except when other agencies as forces have acted upon it, while mind has been believed to be the source of life and endowed with inherent energy. What is energy? The books do not make it clear. To say it is ability to do work is not to define it, but to tell what it can do. Wind, water, steam, electricity, a horse may do work, but no one of them is energy; and energy is not known in experience when disembodied, that is, outside of some substantial thing, and then only shows itself in the degree and kind of activity of that thing. It is in all of our experiences an exchangeable commodity, but there is never an exchange except a mass of matter of some degree of magnitude is present, and conditions the exchange either in character or amount. There is no physical thing which possesses it and is able to impart any of it to another thing without an equal loss to itself. Yet the above conception of something with inherent energy, able to move other bodies in this way or that, without being depleted in its store, implies as much. To make the matter clearer, suppose a mechanical engine to be thus endowed with energy inherent in it and able to act without loss; evidently it would be what we would call a perpetual motion,—would give power indefinitely, and that without any supply for its expenditure. It would mean an infinite source in a finite thing, and a finite thing which can do an infinite amount of work. If this be considered as an attribute of mind, that is, such a mind as humanity exhibits and which each individual of us is assumed to possess, then each one of us would so far be independent of antecedents, and would need no other resources, which is contrary to our uniform experiences. It should be noted that this cannot be considered as a matter of degree, that is, ability to do more or less, for the smallest thing or object possessing ability to do work of any kind without a physical supply from some other source can do an infinite amount of work in an infinite time. The whole has to be granted or nothing. If we are to eschew romancing and interpret phenomena in accordance with our uniform experiences, that is, scientifically,—for that is scientific method,—then it seems plain that one must surrender the notion that life and mind energize ordinary matter which is otherwise inert or dead. There is something wrong in one assumption or the other as to the nature of mind or the nature of matter or possibly both.

What reason has been given or can be given for supposing that matter, as we know it, is inert and incapable of doing anything? There are two answers to this, one coming from religious or theological sources, the other from a physical source; the former probably derived from the story of the creation of living things wherein special creative acts were needed to endow matter with life, and a second creative effort to endow a living thing, man, with a soul. Such a view assumed that matter had in it neither life nor mind, and therefore considered it as both inert and inanimate. Each particle was imagined to be a minute something created out of nothing. Its properties were not inherent in it, but were imposed upon it, and might have been different if the deity had so willed. Of the latter it is to be said at the outset that physical philosophers have almost always accepted their first principles from theologians and have aimed to the best of their ability to interpret phenomena in accordance with such assumptions. It was so in astronomy, in geology, in physiology, in biology. Because no one ever saw a stone or other so-called inanimate object roll up hill, or do something which an animal might do, it was thought to be unable to do anything, whereas every one knows and always has known that it would roll down hill without any agency different from its own; also that one of the laws of motion affirms that action and reaction are equal, and if one kicks such a stone, it will kick back in return. Experience of each one of us teaches the temerity of the action. A lump of coal and a loaf of bread might lie in one place indefinitely long; but would that imply they were inert things and without energy or ability to do anything? No; it would only imply that whatever energy they might have would not show itself by a change of position of the whole body. The loaf of bread is made up of particles of carbon, hydrogen and oxygen with a trace of phosphorus, sulphur, lime, and three or four other elements in less quantity still. If eaten by an animal it will furnish it with energy for doing various kinds of work. If fed to a steam engine in a like manner it will raise weights or propel itself. If it *furnishes* energy it must be because it *has* energy; and if it has energy it is not inert. In a like manner the lump of coal has energy, for, if fed to a steam engine, it enables the latter to do its work. If the lump weighs a pound it is capable of doing ten millions of foot pounds of work, which, if applied to itself, would raise it two thousand miles high. Can a body which possesses such an amount of energy as that in any form be called an inert body? The trouble in thinking of such phenomena is here. Evidences of energy have been looked for only in the ability of a body to do a certain thing, namely, change its position. Let a man be sleeping soundly and he does not change his position. If he is to be moved, others have to do it, but no one would think of calling a sleeping man inert. For the time being he is unable to use his energy in that particular way, and energy may exist in many different ways. The smallest particle of coal we can see in a microscope possesses its proportional part of energy of that kind, and one must perforce assume the same things true of the atoms of carbon; but that is the same thing as saying that carbon atoms are not inert things, and the same thing is to be said of oxygen, hydrogen, and the rest. And there is no evidence that any kind of a physical process could ever extract all its energy, for there is the best of physical evidence that atoms of all sorts are not only indestructible by physical processes, but that they possess inherent energy, and are also able to absorb other energy to a perfectly unlimited extent from the medium in which they exist, namely, the ether; also that they react upon the ether because of their own inherent energy. Observe in all this that I am talking about matter in its atomic forms, not as foreign bodies acted upon by this or that kind of energy, but as being themselves the very embodiment of energy and reacting in every case in accordance with the law of energy.

Physical philosophers had sufficient data for all this long ago, but their philosophical preconceptions prevented its significance from being seen until Joule, Faraday, Helmholtz, and a few others developed what is called the doctrine of the Conservation of Energy. Even with all the evidence we have to-day, there are many physicists and chemists who follow afar off. Some are afraid from religious convictions, others are not interested in fundamental questions at all, and so pay no attention to them; still others are muddled with terminology, which is frequently misleading, and such try to convince themselves and others that not so much is known as is known. The outlook is not such as they expected, and the interpretation is so far from their hazy ideals that the new knowledge and all its implications are repudiated without being apprehended. If matter and its relations are not what they have been believed to be, and if the growth of knowledge has been steadily away from the older conceptions, so that not a single one of them has been verified in physical science, there is left the strong presumption that the remainder will turn out to be as far from the truth as have those which are already settled, if, peradventure, anything can be said to be settled.

Perhaps most persons who are satisfied with the modern doctrine of phenomenal relations and are willing to concede that our notions of the constitution and nature of matter needed revision, and who do not object on any ground to the physical interpretations and explanations, may feel and say: "Granted all you say about the whole of physical science, that matter itself is not what it was thought to be or to be like, even to the extent of being alive in some measure, it would not follow that matter as such could feel or think or know, and this is what the whole contention is and has been about, not whether the physical constitution of things is thus or thus. There is no evidence that matter as such is intelligent." This is a judgment as to the nature and possibilities of matter based on some *a priori* philosophy, not upon a study of the thing itself. Who are they who make such an assertion? Those who know most about matter and its possibilities? Any one who could stand an examination upon the subject for five minutes? I think not. Such may have feeling but not knowledge for this belief. If one is to explain phenomena on the basis of what is known, if all kinds of phenomena are necessarily interrelated, then it is proper to ask if there be any evidence that such activities as feeling, knowing, thinking, exist apart from material structure? As a matter of fact is it not entirely true that wherever there is evidence for either there is abundant evidence for material structure? If such matter be inert, as has been so long assumed, then it was a fair inference that something other than its own resources must be summoned in order to account for any kind of a happening. If, on the other hand, matter be not inert but endowed with energy, then what matter can do and what may be expected of it need further looking into, as is indeed the case.

If what I have presented has any proper warrant in fact, there is then a warning to be heeded against assuming on limited knowledge what are the possible properties of matter and asserting what it cannot do. The difficulty of forming any conception of how such unlike phenomena as feeling and material movements can be related is great, but we have plenty of evidence that we have grown into conceptions which are apparently as unlikely as these. For instance, what possible relations can there be between turning a crank and that which is called electricity, which travels in a wire or in an empty space with the velocity of 186,000 miles a second, glows like the sun in an arc lamp, and will serve for a chat with a friend in Chicago as if you were face to face. Yet there is now known to be a direct and quantitative relation, and the explanation of the whole thing lies in the properties of the atoms themselves — properties which were unimagined not a long time ago. So as knowledge has advanced the whole drift of it has been to enlarge the possibilities of matter itself, and this reflection serves to make it more and more probable that all the other phenomena exhibited by matter are due to its inherent qualities. We must wholly discard the old view of it and adopt a larger view. One must ask again what is the possible nature of matter, and can any one tell enough about it to help on a step in the process, — especially to bridge such a chasm as appears between mind and matter?

We do have a new conception of matter which is now so well vouched for that both the physicists and chemists are interpreting phenomena by its means. This is that the atoms of matter are vortex rings in the ether and made of ether itself; they are simply whorls of ether and are not something else created in ether, and all the properties it manifests are due not more to the structure than to the stuff it is made of; and if this be the fact, the whole controversy concerning matter and its properties and possibilities becomes a controversy about something else than matter, namely, the ether. It is discovered that the characteristics of matter do not belong to the ether, and that nearly, if not all terms we use to describe matter phenomena are wholly inapplicable to the ether; indeed, we are without proper terms to describe them. Matter as we know it is made up of particles; ether is not. Matter is more or less porous; the ether is without interstices,—it is called a continuous medium and is boundless in extent. Matter is subject to friction, and all mechanical movements of it are soon brought to rest. The ether is frictionless. Matter has gravity; the ether is without it. Hence it is plain that one must not include ether when he is talking about matter, for it is altogether a different something with different and unknown and undiscovered qualities, and no one has been able to deduce the properties of matter, as we know it, from the properties of ether. It is plainly the agency by which light and heat get to us from the sun and stars, by which electric and magnetic phenomena become apparent. Gravity is chargeable to its pressure instead of to the attraction of matter. It transmits wave motions at the rate of 186,000 miles a second, but it transmits gravity more than 200,000 million miles a second. Some of the phenomena it exhibits seem to show it to be an enormous storehouse of energy, — one million horse power per cubic foot is a low estimate for it. Like astronomical distances and magnitudes it may be computed but not conceived. With all this it is entirely incapable of affecting any of our senses. We are without any nerves capable of perceiving it, and belief in the existence of such a medium has been forced upon men of science because, first, every former supposition has experimentally broken down; second, because, as Sir Isaac Newton said, it is impossible to think that one body can act upon another not in contact with it without some kind of a medium between them; and lastly, because energy does get from one body to another in the absence of ordinary matter, as is exhibited by the heat and light of the sun, and the rate of transference can be measured in several ways. The interpretation of the physical facts observed has necessitated it, and by its means otherwise inexplicable difficulties are overcome. I think there is not a physicist of any nation or rank who has attended to the facts, who is not satisfied of the existence of what we call ether, but no one can describe it or tell how it can and how it does act upon matter. We are in almost total ignorance about it. If it is hazardous to set limits to the possibilities of matter with the advantage of what knowledge we have of it, what shall be said of the attempt to limit the qualities and possibilities of what we know nothing about, — ether! The mystery of matter is great, but is nothing to the apparent mystery of the ether; and if matter be, as I have hinted, a particular form of energy in the ether, then what can happen in matter depends upon the wholly unknown possibilities of the ether. Again, if the phenomena exhibited by matter lead to the conviction that the latter is made up of the former, then logic leads to the necessary assumption that the ether must have existed before matter, which is made out of it, and so far such a conclusion finds favor with all philosophers. In physical philosophy a phenomenon is said to be explained or interpreted when its antecedents are all pointed out. When such antecedents are unknown we strive to discover the missing factor, always assuming that whatever it may be it has some *necessary* relation to the phenomenon which, when discovered, may be made intelligible in the same terms the rest have been. Note how this applies to the explanation of the existence of matter itself. A uniform, homogeneous, frictionless, gravitationless medium, such as the ether appears to be, could not itself organize a single vortex ring possessing energy, which should be the indestructible thing an atom appears to be. Mechanical actions such as belong to our scientific scheme of knowledge are absolutely powerless in a frictionless medium, and in order to produce such a thing as an atom there is needed an activity altogether unrelated to any kind we know or which has ever been the subject of consideration in physical science. Creation is the only word which is suitable for the action, and there is implied behind the ether some other factor *not necessarily related* to it in the sense in which ether is related to matter. So that behind both matter and ether there is a something which must be postulated as the initiative of all we see and know, capable of acting upon the ether, but *without mechanical compulsion.* Therefore choice, a mental attribute, has a locus here, and mind appears to be a necessary assumption, as necessary for a proper antecedent as is ether pressure for the phenomena of attraction or an artificer for making a house, and this, too, wherever there is an atom, whether here upon the earth or in the most distant star, — everywhere, omnipresent mind. Choice implies consciousness and intelligence, and so physical interpretations of the phenomena always before our eyes lead us back to a superphysical beginning. If we find energy in the form of matter, it is not necessarily there. If we find life in it, it is because mind is operative in all ether and therefore in all matter, and cannot be exorcised from it. Some philosophers speak of this as "infinite and eternal energy," but it is not such energy as the physicist measures in foot pounds. Other philosophers call it God, and can one express in terser, truer or more scientific language the relation of mankind to this infinite power than did Paul in Athens : "In Him we live and move and have our being."

SIXTH LECTURE.

KNOWN RELATIONS BETWEEN MIND AND MATTER.

A. E. DOLBEAR.

We have a body of knowledge which we call science. In a few — a very few — instances it is so far perfected we can use it for prevision, and thus we make almanacs, learn when the moon will be eclipsed, and when the tide will come in, how to make a steam-engine or a dynamo to do a specific amount of work, and so on; but for nearly every question in which humanity, as a whole, has an immediate interest there is now no satisfactory answer, which, broadly stated, means that there is yet no science which can be applied to them in the same sense as it can be applied to astronomical problems. The best one can do is to hold any opinion very gently, and be ready to abandon it at once if occasion comes.

"The science of life," — that is what we all want to understand in order to get the most out of it. That there is a possible science of life everybody believes. In every great emergency among men there are always a number of persons who are ready to tell us about it, and what should be done to avoid catastrophe. When Jerusalem was in a state of siege there were several who claimed to be the Messiah, each promising deliverance if the people would but hearken to them; but in the multitude of such Messiahs, how could one judge which was the true one except he should actually deliver them from their troubles, whether they believed in him or not? The test for one's ability is what he does, not what he promises to do. So there are teachers and preachers and makers of books who tell how it is, and what to do, yet we are no wiser, and society is troubled with trusts, monopolies, strikes, theories of taxation, of protection, of values, of liberty, of free-will, of the family, of education, of heredity, of life itself; and who shall deliver us? To say that science will may be true enough, but she cannot to-day.

In his *Locksley Hall* Tennyson wrote more than fifty years ago:—

> "Science moves but slowly, slowly,
> Creeping on from point to point."

And that was true then, and in large measure is true to-day, concerning all those matters that relate more nearly to us in our everyday lives. When we laud science, and tell how much has been accomplished within the past fifty years, it is just as well to remember that what has been achieved in this domain has been mostly in the purely mechanical field. We feel quite sure we now know how the Solar system came to be as it is,—through a series of slow changes by which a huge molecular cloud of dust in space becomes a body of rotating globes revolving about a central hot mass. We feel quite confident that what we call the doctrine of energy is true, and that it is not created or annihilated by any processes in our experience. We are almost, if not quite convinced that the animals and plants upon the earth to-day are the descendants in unbroken line from the simplest microscopic forms of living things in the far off geologic ages, and we put all these things together and call the process of becoming something different, —*evolution;* and for convenience we call some mechanical science, and some molecular science, and some biologic science, according as the subject-matter is among big bodies or little bodies or living bodies. But it is sometimes forgotten or overlooked that the same forces are at work with the little as with the big bodies, and that no body, large or small, can be separated from the action of all the rest, and that no particle of matter ever lets go its grip on any other one. These things, I have said, we think we know; but may I not say we *do know*, if we really do know anything? If there be any doubt about gravitation, about the laws of energy, about the multiplication table, then one may harbor doubts about any thing he pleases;

and there is justification for even this doubt. Have not the mathematicians lately told us emphatically that there are no axioms, that all once held as absolutely true about lines and angles — in short, geometry — has no better basis than experiment and the narrow limits of our experience, thus bringing our rational powers to a standstill in the presence of problems out of the range of our instruments? This is precisely what has been done, and for all we know the universe may be a very different thing from what it has seemed to be, for in concluding what it is we have always assumed that space was what it seemed to be, and that ideally one could go in a straight line on and on forever. Now we do not know that, say the mathematicians; and they talk of space of four or more dimensions where our laws of physics and energy will not hold. And more than that, some of them begin to derive comfort from the reflection that, after all, the universe is not half so simple and easy to understand as they had once thought, and that the possibilities of knowledge and of existence may vastly exceed anything any one has yet imagined. For us, then, science must be *correlated experiences*, and for us the truth can only be that statement which is in accordance with the best and most certain other things we know; it must be in accordance with our geometry, our energy, with our modes of thought, and then always with the reservation that what to-day seems fundamental may ultimately turn out to be derived, and relations that seem obvious may be far from it.

All this is a sort of disclaimer against being taken for one who believes and teaches that the knowledge we have is sufficient to enable him or others to deduce all phenomena, or even to foresee in any kind of way how to answer properly many of the questions which concern us all. The decalogue was mostly a compendium of *don'ts*, and the best that such science as I have knowledge of can now do is to tell us what not to do, rather than what at once to do, and gives a mere hint as to the direction one must look for further light on any or all of them. Of course we all know how men have speculated on both mind and body and their relation, and it has always been quite the fashion to go into the history of the steps in thought from the earliest time till now when treating on this and kindred topics, — a course which implies there has been some kind of progress, and that each generation has contributed in some degree to the solution. It hardly needs to be said that this is no more true in this matter than in any other of the sciences. In astronomy one need not go back of Copernicus. In chemistry one need not go back of Dalton. In electricity one need not go back of Franklin; in heat, back of Sir Humphrey Davy; in biology, back of Darwin. Not that there was nothing known before them, but what was known was of little and no importance. If all biologic knowledge before 1840 were subtracted from present knowledge, it would scarcely be missed; and if in these fundamental things there was nothing of importance, still more true is it in the more difficult and unexplored field of mind and its bodily relations. There is not a single philosopher from Adam, and the year 1 up to 1850, whose knowledge and opinions on the question are worth a hearing; and all references to the expressed or implied statements of any of them, as having any weight at all in the settlement of any of these questions, seem to me to be utterly useless, — as useless as their speculations on the habitability of the planets. None of them had adequate data; in fact, they *knew* nothing about it. If, also, one remembers that modern knowledge is not ancient or mediæval knowledge confirmed and expanded, but *new* knowledge which contradicts and repudiates most of the old, he will see still less reason for appealing to antiquity for the support of any doctrine. Now, seeing that the theologians have admitted that the Bible was given for instruction in religious things, not in science, it is no longer safe to quote scripture as a warrant for any opinion upon a question involving scientific data or method; hence, even on the question of mind and body no one looks there either for direction or corroboration.

By body we mean the matter which constitutes the animal mechanism, as that which embodies the various functions of growth, assimilation, movements of one kind and another, and along with these exhibits, in some degree some order of intelligence. Once there seemed to be sufficient reason for dividing living things into plants and animals. That was when knowledge was fragmentary; but now there is no line between them, and no naturalist can so define one as to exclude the other. The possession of what is called irritability, by which is meant ability to respond by movement of some kind to an external stimulus, is no longer a peculiar characteristic of what have been called animals, for there are many plants that possess it in a marked degree; and there are free swimming plants, such as bacteria. Experimental research with the microscope has shown that this quality exists in all plants in some degree, and that in all cases the reaction, of whatever kind it may be, shows evidence of what, in higher forms of living things, is always attributed to intelligence; that is, the reaction is adaptive. This does not mean what in higher living things we call choice, but it does mean that the energy resident in the organism works spasmodically, automatically, and mechanically in a very wonderful manner, and gives rise to phenomena which have been thought could only appear where there was some kind of animal existence as distinct from a vegetable. The discovery of sensitivity as a quality belonging to *all* plants is new, and makes it still more important that one should inquire further as to whether other distinctions are as real as they have been thought to be. Once a vital force was believed to be resident in living things, and this force was supposed to control digestion, nutrition, growth, and feeling, but all biologists have discarded the idea. I do not know of a single naturalist of any distinction in the world who does not think and say that all the phenomena exhibited by plants and animals are due to physical and chemical causes alone. In a late lecture Professor Stokvis, of Amsterdam University, said: "Certain it is that life is a chemical function," and he thinks it is proved beyond a peradventure. To present the evidence for it would be to make a book; and seeing that it is so generally accepted in scientific quarters, where it would first meet opposition if it could be opposed, one may accept it, — at any rate, provisionally.

But what is meant by life? Well, in brief, it means the sum of the activities possessed by living things, including growth, assimilation, reproduction. If such qualities are really *only* refined physics and chemistry, as has been stated, then is it much matter for wonder that our predecessors did not find it out, seeing that they had no knowledge of either? Now, the outcome of what is called life, even in the lowest and so-called insensate forms, is wonderful enough, and is so different from what has been supposed to be possible to mere matter, that it is worth the while to stop and consider why it has seemed so different.

The philosophers in all the past have had a kind of theory of things to maintain, as to how man came to be on the earth, and especially how evil came to be his portion. Man was created upright and good, but by transgression he fell, and the earth with him was cursed. This theory required the conception of the matter or material of which the earth is made as being utterly inert and dead. The idea was that life, as we know it, was breathed into it, and not until then was there any living thing. Matter was not only lifeless, but it was gross, and all sorts of epithets were applied to it to make wider the distinction between it and a living thing. From a dictum it became a belief; and, although there was no one who could prove it, or took any steps to prove it, it came to be considered true, and the proposition that matter had no power to do anything by itself was thought to be almost axiomatic, and that in spite of the wonderful succession of all kinds of phenomena witnessed every day, — combustion, the falling of an apple, the formation of clouds and dew and hail, the recurrence of day and night, the explosion of powder, of gas, and others just as well known, all showing that matter, so-called inorganic matter, did in some way possess active properties of certain kinds by which it could change phenomena solely through its own powers. It *is* endowed with energy. Mix sulphur, carbon and saltpetre together — the mixture you call powder; but you are aware that the compound possesses tremendous energy which you have not imparted to it; and so does all matter — every atom of it — possess energy of a kind that enables it, under proper conditions, to do the most wonderful things; and yet this was not suspected for thousands of years, and even after it was discovered it was not perceived for a long time that the inertness of matter could no longer be held as a tenet in philosophy. There are plenty of teachers yet who think matter to be inert, and as possessing no energy. But what is energy? Simply the ability of a body to act on other bodies so as to move them in one way or another.

That kind of action which is called chemical action, by which atoms combine together in certain definite ways, in which atoms choose their partners and become wedded, is a manifestation of the energy of atoms, which is ever present with them, a part of their endowment and inalienable. Heat, light, electricity are modes of the energetic action of the ultimate particles of matter called the elements. In all the manifestations of these so-called forms of motion or energy, which we employ for economic uses, it ought not to be forgotten that we do not endow the matter, but we find it already endowed, which shows that matter is not to be considered as so helpless as it has been the custom to think it to be. But these atoms and their combinations—that is, molecules—are often found organized into beautiful forms called crystals. There are diamonds and sapphires, rubies and emeralds, garnets, topazes, beryls, sugar, alum, and a thousand forms familiar enough everywhere. These symmetrical forms are due solely to the inherent qualities of the substances themselves, and testify to the ability of the matter to *arrange* itself, which *inert* matter could not do. Dewar and others have shown that in the absence of temperature, chemism does not exist; and if matter can do so much as is plain to perceive, is it likely that these exhaust the possibilities of its doings? We know better already; but I have developed this point far enough to show what I want to make plain, namely, that matter has possibilities which the reigning philosophy has denied it to have.

It has been the custom to speak of all the inherent qualities of matter and the various phenomena which directly result from them as being physical and chemical. Are there any such purely physical and chemical phenomena that are really comparable with what we take to be vital or living phenomena? Yes, a great many.

Let a crystal, say of quartz, have an end or a corner knocked off. If it now be placed in a solution so that growth can go on, the crystal will mend up its defacement so as to be symmetrical before it will be enlarged elsewhere, just as a spider will grow a new leg if the old one be removed. The cases are similar. There are so many and so great a variety of such activities in matter that, from the physical side, men have been forced to conclude that *matter is itself alive*, every atom of it, just as the biologists from that side of the study have concluded that life is a chemical and physical process simply. There is agreement here. With such a conception of matter, one cannot look at any object whatever without increased respect for it, for not alone the animal or insect which is called living possesses the distinguishing vitality, but the very air we breathe and the dust under our feet. The food we eat endows us with life because it has it, not that it creates it. We eat it and drink it and breathe it, and withal, life in this view is here and always has been. There is no need for a miracle to populate the world, and every star and satellite is inhabited,—yea, is a living thing itself, the degree of complexity of such life depending solely upon the possible complexity of chemical organization. This is an inference, of course, but it follows from the premises without any circumlocution.

By body, then, we mean a local habitat for a living thing. We also mean the living thing itself, whether it be large or small; and seeing there is no special limit to the magnitude of a body which possesses this quality, and that there is good reason for holding that matter is itself alive, it is apparent that it is now of importance to know still more of that thing we call an atom, whether it be of one kind or another. We all know what the text-books say about its properties, as of weight, hardness, density, elasticity, impenetrability, and so on. It will be remembered, also, there are known some seventy different kinds of elementary matter. If one will stop an instant to think, he will see that differences in size or shape cannot account for such differences in quality as are presented by the elements. One might make of wood seventy different sizes and shapes, but the density, hardness, elasticity, and so on would be the same in all. So there would be needed as many kinds of elementary stuff out of which the atoms were made as there were kinds of atoms, and this complicated process and material has no degree of probability at all, for the physical evidence we have an abundance of to-day all goes to show that nearly, if not quite, all the physical qualities of the elementary atoms is due to the quality of their motions and to nothing else. There is not time to enter upon this phase of the question, but it is true that physicists have been led to this conclusion which I quote from Karl Pearson's work on *The Grammar of Science:* "The whole tendency of modern physics has been to describe natural phenomena by reducing them to conceptual motions"; also, "Hardness, weight, color, temperature, cohesion, chemical constitution may all be described by the aid of the motions of a single medium which itself has no hardness, weight, color, temperature, nor indeed elasticity of the ordinary type." If such a view of the subject-matter be true in any sense, then one sees at first glance that what one means by body — that is, visible masses made up of this kind of matter — must be very different from what is involved in the ordinary conception of it, and life must be very different in its nature from what it has so long been held to be. As such matter as is described above cannot be created nor annihilated by any physical or chemical process yet discovered or even imagined, its very existence is a guarantee of all of its so-called qualities, even life itself, and we come in sight of a fact of tremendous importance to every individual who has tasted the sweets of existence and who feels loth to give them up, especially when he sees creation is so large, its possibilities of gratification so boundless, that probably millions of years have been spent in leading up to him, which, if he is to cease conscious existence at any time, will apparently have been wasted with little or no profit to any. Some have hoped that what is called this life is not all, and they point to this or that as evidence for their hope, but there has been a total lack of physical evidence for such an issue. No one who knows anything about matter doubts that an atom of, say carbon, is practically an indestructible thing; that its properties were the same a million years ago as they are to-day, and will be the same a million years to come; and if one knew it to be a living thing now, he would expect it to remain a living thing, and if it were conscious, that it would continue to be conscious. Another important consideration lies here. The so-called properties of matter are not detachable from matter itself. One cannot separate heat or weight or vitality from a mass of matter; they are not entities, they are qualities. Set a top spinning and how wonderfully it behaves. It will stand on its point and hum, or sleep, as the boys say; but touch it ever so gently, and how it will bound away, and do the most unexpected things. It is the motion it has which enables it to act thus, and one who did not know that the sleeping top was in motion, and should notice what it did on being touched, might fairly well think it had a spirit in it. But no one can detach the spin from the top so that he could hold the spin in one hand and the top in the other; neither if life be such a material property can it be detached from what embodies it. If one ties to physics at all he must not play fast and loose with it. It will not do to take this and reject that because it does not meet our likes or wishes. There is no evidence I am acquainted with that physics acts *conjointly* with anything else. Whatever it does, it does on its own responsibility, and the result is to be measured on its own balance. This is equivalent to saying that the field of physics is much broader than has been supposed. When Newton lived, physics had to do only with the movements of large bodies. In our time it has been carried down to atoms, and, as I have said, the knowledge here gained has been not simply an extension of the old, it has been revolutionary in its bearing on all questions, and the glimpses it has given of present outlying fields convinces one that there must soon come such a hegira from the old schools of thought as has never been witnessed, although the past thirty years shows that in the field of natural history everybody has changed from a creationist to an evolutionist. But this has been only the beginning of the change, for if that science was true that made such a change necessary, it is also true that the same science will make needful other changes in men's conceptions of what kind of a universe they live in, how it works, and how they came to be and to think as they do; and not unlikely what we please to call evolution will have to be explained and restated in very different terms from those in vogue now.

So far I have talked about body and have endeavored to show that present science gives no warrant for holding that the matter which constitutes it is lifeless or inert; but, on the other hand, it does show that it is endowed with energy, and that in enormous quantity, and also that the minute study of it has led students from both the biologic and physical side to conclude that matter is itself alive, as endowed with an inalienable quality, and that the manifestations of this quality depend upon the degree of complexity of composition and arrangement rather than upon any superendowment of any kind of an entity, and hence giving no support to the notion of a disembodied spirit, in the extreme sense of that expression. How much matter is really needed to exhibit any degree of life?

Let us turn now to the other factor, — mind. First it may be remarked that there is no tangible evidence of the existence of mind apart from some kind of a material structure. I suppose there is no one now who would imagine that in the development of, say a chicken, there came a time in the physical and chemical changes going on in a warm egg when it was in some superphysical way endowed with what we call mind in any degree, so that one could say, *now* this growing thing is without mind, and the next instant, *now* this growing thing has a mind. If mental endowment be not a part of the physical process just as necessary under the conditions as any other part of the process, then one *must* say at some instant, *now* it has been endowed. The chicken in the egg has life, for it grows, and when out of it gives evidence of intelligence of no mean grade. Whatever its grade, it is the outcome either of its physical constitution or else there has been a miracle of some order. Is there any third alternative? I know of none. That there has been a miraculous phenomenon in the egg, no one can believe, and that the intelligence is the mere outcome of physical antecedents few want to believe. If one believes that humanity, as it now is, is traceable without miracle into geologic times, that in some kind of a way all degrees of intelligence are directly related, then what in its degree is true for a chicken is also true for man, and mental endowment is no more miraculous for one than the other; and one must need to look for his so-called faculties where he must look for those of the chicken or the dog, namely, as the outcome of the original endowment of what we call matter, rather than as a supernatural alliance with matter which is the common notion. Already enough is known as to the material dependence of the mind upon the body to warrant even judicial acts to be based upon chemical analysis of bodily products; that emotions of different kinds yield corresponding chemical substances. Some of these products are harmful in the extreme, some poisonous, while others are healthful and promotive of life. Brain building is the end towards which this new science is reaching. One of its axioms is that the mind can only be educated through the senses, and the more senses and the better they are developed the more mental power. Thinking is the function of gray cellular matter that covers the brain like the rind of an orange. Unconscious thinking vastly exceeds in amount our conscious thinking. When thinking and doing have been repeated often, they cease to be conscious acts, — they become automatic, instinctive, and seem to sink out of conscious personality; but they may be summoned. So that unconsciousness makes the most part of our lives. The individual starts with a bundle of instincts, that is, inherited experiences, all unconscious, but yet the product of consciousness; and consciousness that has all come from and through nerve action. All this may be so, and yet the question still could be asked, are mind and matter separable? One might point, as others have frequently done, to the evidence of the growth and decadence of the mind along with the growth and decadence of the bodily functions, of the impairment of mental activity and quality when the brain or stomach or liver is impaired, and full recovery when these are brought to normal conditions again; also how the individual lives over in himself the history of the race, as a mere animal at first, then a savage, and lastly as an intellectual and moral being, — a condition of things that educational theories and practice ignore or overlook when they attempt to make a moral and intellectual being out of one in his savage stage of existence, as if one should try to make the caterpillar live on the honey of flowers and fly, when as yet it had neither the instincts nor machinery for such a life. Feed him what he wants and can digest, protect him from enemies of all sorts, and let him otherwise alone. If nature intended him to fly, his wings are growing, though they may be folded so as not to be discerned and no use is made of them. Let them alone. If she did not thus intend him to fly, no food nor training nor painstaking will give him wings and he will never fly. This is a by-path.

To everyone who has thought and read on this subject of the relation of mind to the bodily organism, especially in the last few years, there appears at once the question of the relation of the doctrine of the conservation of energy to mental action, the question of free will and the question of automatism. I have not heard that any one actually disputes the doctrine of the conservation of energy, which means that energy is not created nor annihilated by any kind of a process known to us. Let me quote the words of Höffding in his *Outlines of Psychology* as bearing on this point : "In the nature of the case only four possibilities can be conceived : (1) either consciousness and brain, mind and body act one upon the other as two distinct beings or substances, (2) or the mind is only a form or product of the body, (3) or the body is only a form or product of one or several mental beings, or finally, (4) mind and body, consciousness and brain are evolved as different forms of expression of one and the same being." He then presents the arguments *pro* and *con* on each of these, and at last thus concludes : "Only the last or the fourth possibility then seems to be left. We have no right to take mind and body for two beings or substances in reciprocal interaction. On the contrary, we are impelled to conceive the material interaction between the brain and nervous system as an outer form of the inner ideal unity of consciousness. Both parallelism and proportionality between the activity of consciousness and cerebral activity point to an *identity* at bottom," and he italicizes *identity*. Such statements from such a source show that even psychologists of the experimental type have been driven to conclude that mentality and physical activity are not different things, but opposite sides of the same thing, which is saying in another way that mind is as much a function of matter as is gravitation, or as magnetism is of iron, — cannot be created nor destroyed nor isolated, but may be obscured in various ways. To say that one cannot conceive how mind can be so related is not to say much. Can any one say he can conceive how mind, as he imagines it, can exist in a body at all? And does one need to wait until any matter is fully explained before he can assent to what is known about it? Thus the existence of dynamos and motors and electric lights and telegraphs and telephones is in itself sufficient to prove that we know a great deal about electricity, the conditions for its generation and utilization; and when one adds to these the knowledge that dynamos and motors can be made at will, having an efficiency of 96 or 97%, he has as high a guarantee as one can have for anything in this world that no man hereafter can improve on our electrical apparatus by as much as 5%, and all this without pretending to know or even guess *how* it is that electricity can do anything, much less have a knowledge of its ultimate nature. These may come in due time. Meanwhile one need not be skeptical as to how much is known — really known — about it, because he cannot answer the very last question which may be asked about it.

What, then, is the present status of the question? In our experience mind is associated with matter always, life as we know it is always associated with a particularly complex chemical substance; and when, for any reason, this substance of life is disintegrated, the evidence of life goes too. The more complicated the material organism, the more complicated the manifestations of life and of mind.

The delight in the consciousness of existence has led man to wish for its continuance and to cast about for evidence of it. The apparent destruction of mind with the disintegration of the body has led men to think there must be some fallacy somewhere; and so they have asserted that the body is but a temporary habitat for the mind, or soul, as it is often called, and that the soul could and did exist independent of matter in any of its embodiments, so the conscious being has been imagined as an immaterial something, very much as heat and light and electricity have been supposed to be immaterial somethings. By and by heat and light and electricity were each shown to be no such kind of things, and as having no existence apart from ordinary matter. After that, vital force as differing from chemical and physical forces was dispensed with, and next both biologist and physicist agree that life is, in all probability, but a function of ordinary matter; and lastly the psychologist brings in as his return that mind and matter are but the two sides of the same reality. This does not mean what it has generally been taken to mean, but exactly the opposite. It has been held and taught by many that to associate either life or mind with matter as a necessary adjunct was pure materialism. Some have thought that if the doctrine of the conservation of energy were true or were admitted to be true, then life would be correlated with the other forces as they are correlated with each other, so that whenever one appeared it was at the expense of and destruction of some other, — as when heat energy is changed into work or into electrical energy. But the analogy is wrong. It would be nearer correct to liken it to, say magnetism of a piece of iron. For convenience we say we magnetize a piece of iron. In reality we do nothing of the sort, — the iron is already as magnetic as it can be; all we do is to arrange its molecules so that the inherent magnetism of each one will act in the same direction as all the rest. There is as much magnetism in a piece of iron at one time as at another; we cannot change that. To carry out the analogy, if one would suppose that when the atoms and molecules of matter are of proper sort and arranged in a proper way, as they are in the substance called protoplasm, then the individual living characteristics of each could manifest themselves in the way exhibited by a living thing, not because there was a new force or being or entity not there before, but because all could work in concert to the same end, while they cannot under ordinary physical conditions. In other words, there is nothing which was not there before. One is not getting out of the machine what was not in it, but what was in it, and there is no quarrel with the doctrine of the conservation of energy. That doctrine, if true, would only insure continuity, regularity, and certainty of dependent relations.

Still more than this. It is important to recognize how much energy there may be in a microscopic mass of matter, and also what an amount of intelligence may be there too! Think of the intelligence shown by a common ant: he lives in a community having common interests, and where the duties of individuals are appointed and faithfully executed, — duties of securing food, of protecting and caring for the young, of defending the community as a whole. They make war, and slavery is the price of peace; they have a language of some sort and a degree of civilization superior to some tribes of men, and all this the outcome of a brain so small that no balance we have is delicate enough to weigh it. It is plain proof that if mind does require some material habitat, its requirements are not excessive; indeed, if one will remember that in a mass of matter only the thousandth part of an inch in diameter there are thousands of millions of atoms, he will see that the possibility of variety of form, of position, and of relations is almost infinite, and if mind depended upon these in any measure, the possibilities would also be nearly infinite. There is nothing in all this that implies that what is called death ends all, — rather the contrary, for it is plainly in accordance with all we know to hold that the so-called *ego* is a real material thing, a molecule too minute to be seen or identified, but which absorbs all experiences and holds them as memory, which can be dissociated from the rest of the body, but which cannot itself be disrupted any more than atoms of the ordinary sort can be, which is as durable as we believe others to be, but differs from them chiefly in having been *educated* by being in such a position that all sorts of reactions took place in its environment and in itself.

Formerly mind was supposed to be honored by degrading its material habitat; now we are confronted with the knowledge that matter is not what it was thought to be or to be like, that its nature is as mysterious as is the nature of mind. In experience we find the two always associated. Experience leads to the belief that one of these is imperishable, and we make it a corner-stone in physical science; and my thesis is that mind can no more be sloughed off from it than can gravity or magnetism or any other of its inherent qualities.

SEVENTH LECTURE.

ON THE PHYSICAL BASIS OF ANIMAL PHOSPHORESCENCE.[1]

S. WATASÉ.

WHATEVER view we may take as to the nature of vitality, it is evident that we can know life only through the physical, chemical, or mechanical manifestations, which an organism displays at various phases of its existence. Our organs of sense, which supply directly or indirectly the material of human knowledge of both the animate and inanimate world, are only related to force, or are set into a state of excitation by motion of certain kinds, which we call a stimulus. Whatever view, therefore, a biological philosophy may lead us to accept in regard to the ultimate nature of life, our primary step in the study of vitality must begin with the examination of its material manifestations.

Among many physical phenomena manifested by the living organism there are few so striking, and none appear so isolated, as the phenomena of the emission of light. Thus, Darwin, in his discussion of some special difficulties of the theory of natural selection, says: "The luminous organs which occur in a few insects, belonging to widely different families, and which are situated in different parts of the body, offer, under our present state of ignorance, a difficulty almost exactly parallel with that of the electric organs," and "it is impossible to conceive by what steps these wondrous organs have been produced."[2]

[1] The present paper is part of three lectures on Animal Phosphorescence, delivered at the Marine Biological Laboratory at Woods Holl, during the summers of 1894 and 1895, and elsewhere. A monographic account of the subject, with a full bibliography, will be presented in the near future.

[2] Darwin: Origin of Species.

But viewed from the standpoint of cell physiology, the phenomena of animal phosphorescence is the result of physico-chemical changes in the living protoplasm, probably of the same nature as that of heat production, the only peculiarity of the former being that it manifests itself in such a form as to affect the most potent of our special senses, — the sense of sight, — and the latter, the sense of temperature.

On *a priori* ground it is easily conceivable that the animal that produces heat, as all animals can, may just as well produce light under certain circumstances, for both are but the manifestations of the same energy, and can be produced by essentially the same physico-chemical antecedents.

The production of light by the living organism becomes still more interesting, and appears unique when we remember that the light thus produced is not accompanied by any sensible heat.

> "You gaudy glow-worms, carrying seeming fire,
> Yet have no heat within ye!" [1]

This difference between the light produced by the activity of the living organism and by the purely artificial process has also been pointed out by the natural philosopher, Robert Boyle. In one [2] of his several contributions on the subject he says: "That whereas a coal, as it burns, sends forth store of smoke or exhalations, luminous wood does not so"; and "that whereas a coal in shining wastes itself at a great rate, shining wood does not"; and "that a quick coal is actually and vehemently hot, whereas I have not observed shining wood to be so much as sensibly lukewarm." [3]

The same peculiarity in the light of the living substance has been recognized by Faraday, Matteucci, Young, Langley, and Very, and by the last two it has been made the subject of a beautiful research within recent years.

[1] Fletcher: The Elder Brother, act iv, sc. 1, 1637.

[2] R. Boyle: Observations and Trials about the Resemblances and Differences between a Burning Coal and Shining Wood, *Phil. Trans.*, No. XXXII, 605, 1667–1668.

[3] It is hardly necessary to say that Boyle was not aware of the fact that the luminosity of the shining wood is caused by the activity of the living organism.

Readers of the *Life of Faraday* will notice what a lively interest he took in the luminous phenomena of the fire-fly and the glow-worm. The journal[1] he kept during his travel over the continent with Sir Humphry Davy in 1814, when Faraday was twenty-two years old, makes frequent mention of his experiments with the luminous phenomena of the fire-fly and the glow-worm. I quote him at length because he correctly surmised all the results of his later workers, and also because his unassuming but remarkable record of his observations has escaped the notice of writers on animal phosphorescence subsequent to the publication of Faraday's Life. (Italics are mine.)

"On the way home many fire-flies appeared, emitting their transient light.[2] I caught several; and on arriving at the house *endeavored to ascertain whether the luminous appearance depended on the life of the fly.* I found one apparently dead; and separating the part which emitted light from the rest of the body, it appeared filled with a white glutinous matter, which, when extended and exposed to the air, shone for about a minute.

"I killed a fly suddenly, and separated the matter. It was shining at the moment I killed it; but when dead it ceased to shine. On separating the part and exposing it to the air it immediately shone brightly as when attached to the fly, and over the whole surface, although only the section was exposed to the air. It at length became dim; but on compressing it, and exposing a fresh part to the air, it shone brightly as at first, and thus it continued luminous for above forty minutes. At last it became totally extinct; and the same effect took place with other flies treated in the same manner. *It is probable, from the intermitting and regular appearance of the light, that it has a dependence on the respiration; and at least it is evident that air is sufficient to cause this matter (probably a secretion) to shine. No heat was sensible to the hands or to the underlip (the most delicate part of the body).*"

[1] Dr. Bence Jones: Life and Letters of Faraday, Vol. I, 1870, pp. 90, 91, 125, 141, 142, 144–146.

[2] Friday, June 3, 1814 (Terni), Italy, pp. 141, 142.

In his entry "Sunday, July 10, 1814, Geneva," Faraday describes his experiments on glow-worms.

"This evening many glow-worms appeared, and of four which I had put in a tumbler with green leaves, two shone very brightly. I separated the luminous part of one in full vigor from the body. It soon faded, and in about ten minutes ceased to emit light; but on *pressing it with a knife, so as to force the matter out of the skin, it again became luminous, and continued to shine for two hours brightly.* One I found on the floor crushed unawares by the foot. I separated the luminous part of this insect, and left it on paper. It shone with undiminished luster the whole evening, and appeared not at all to have suffered in its power of emitting light by the mixture and confusion of its parts, *so that it appears to depend more upon the chemical nature of the substance than upon the vital powers of the animal; but at the same time, it appears, from the variations in splendor, accompanied by motions in the living animal, that it may be much influenced or modified by, or in some manner submitted to, the powers of the worm.*

"The matter which appears to fill the hinder part of the body in the shining season is yellowish-white, soft, and glutinous. It is insoluble, apparently, in water or in alcohol. It does not immediately lose its power of shining in water. Heat forces out a bright glow, and then it becomes extinct; but if not carried too far, the addition of moisture after a time revives its power. No motion or mixture seems to destroy its power whilst it remains fresh and moist, but yet a portion thus rubbed sooner lost its light than a portion left untouched. The time of its continuance in a luminous state was very various, and perhaps depends upon the state of the worms from which it was taken. The death of the worm seemed to have no immediate effect upon the illumination of the hinder part; and with respect to the length of time that it continued to shine afterwards, it seemed indifferent whether it was left on the body or taken off; but when extinct, exposure of the interior to air always caused a fresh emanation of light. I found a worm which emitted light from a very small part of the body, and very feebly, and for a very short time together. The worm was larger than the ordinary species, and had more divisions. The power of emitting light in the ordinary worm seemed proportionate to the age of the animal."

Monday, 11th. "The matter of the worms referred to yesterday still shines. It was detached from the animal at 8.24, and still promises to emit light much longer."

Tuesday, 12th. "The matter was luminous this day at 10.41, though faintly, and at twelve o'clock no light could be perceived. The matter had become quite dry and semi-transparent, but the addition of water produced no particular effect."

Faraday's results may be briefly stated as follows: —

(1) There is a chemical substance in the glow-worm and the fire-fly which has power to shine independently of the life of the insect.

(2) This substance is probably a secretion of the insect.

(3) The shining depends on the respiration, and the air is enough to cause this substance to shine.

(4) From the variation in the splendor of light, accompanied by motions in the living animal, the animal, as a whole, has in some way the control of the external manifestation of light.

Matteucci, also, in his letter to Duma,[1] and elsewhere,[2] came to the same conclusion as Faraday, and says: "In the glow-worm there is a substance which, without any sensible heat, diffuses a light that does not require the integrity of the animal and of its living state in order to manifest itself with its peculiar properties."

It will contribute to the clearness of the whole, if, instead of examining various other theories proposed from time to time, in the nature of animal light, I dwell briefly here on the relation of objective and subjective aspects of what we call the sensation of light and of heat, or the relation of various kinds of ether vibrations to the specific energy of senses.

We habitually associate the sensation of light with that of heat, so that it becomes almost impossible to separate them in

[1] Carlo Matteucci: Sur la phosphorescence du Lampyre d'Italie (L. Italica). *Compt. Rend.* XVII, p. 309, August 14, 1843.

[2] Matteucci: Lectures on the Physical Phenomena of Living Beings, 1848, p. 165.

our common experience; and when we meet with such a phenomenon as the production of light from the animal tissue without any sensible heat, it appears as if it were a totally isolated physiological phenomenon with no parallel in the ordinary activity of life.

According to the physicist, however, the external agent which gives rise to the sensation of light in our organism is not much different from that which gives rise to the sensation of heat. Heat and light are only the variations of the same radiant energy. There is an absolute continuity in the nature of the two phenomena — the vibrations of ether.

"When the wave-length is greater than 812 millionths of a millimeter no luminous effect is produced on the eye, though the effect on the thermometer may be very great. When the wave-length is 650 millionths of a millimeter the ray is visible as a red light, and a considerable heating effect is observed. But when the wave-length is 500 millionths of a millimeter, the ray, which is seen as a brilliant green, has much less heating effect than the dark or the red rays, and it is difficult to obtain strong thermal effects with rays of smaller wave-lengths, even when concentrated." [1]

The light and heat are so very different to us because we perceive them with different organs of sense. The heat radiation, or the waves of ether which have most *heating effect*, we perceive with the organ of temperature sense, while a similar radiation, with different wave-lengths, which have most *luminous effect*, we perceive with the organ of sight.

The difference between heat and light, therefore, "is purely subjective, depending on our organization and not on the nature of external objects." [2] There is an absolute continuity in the nature of external disturbances which create in us the sensations of heat and of light, the difference between them being that of degree and not of kind. Expressed, therefore, in terms of visual sensation, heat is invisible light; and light, expressed in that of temperature sense, is heat with a very little heating effect.

[1] Clerk-Maxwell: Theory of Heat, Chap. XVI., On Radiation, p. 239.
[2] Stokes: On Light, p. 266.

If our organs concerned in the sensation of light were somewhat different from what they are now, it is possible that what appears as luminous may have no such effect, and what appears as dark may even appear as luminous. "It is quite conceivable that animals might exist to which obscure heat rays might be visible, and to which man and mammals generally would appear constantly luminous." [1]

The animal organism is an actual apparatus of combustion, in which carbon compounds are constantly burnt, and from which carbonic acid is always escaping. There is no difficulty in conceiving that organisms which produce heat in this way may under certain circumstances produce light, if the combustion of the material in the body could be carried on in such a manner as to impart a more rapid vibration to the surrounding ether than that which results in the production of thermal radiation.

The vibration of ether thus produced with higher frequency and of shorter wave-lengths, such as we see in the fire-fly, would affect the organ of vision, but not the organ of temperature. *And this difference of result, so conspicuous to us, may not imply more than a very slight variation on the part of the individual organism at the start.* Nature desires, if I may use such an expression, nothing but light in such an organism as the fire-fly, and produces this with the least possible waste.

That this is a legitimate inference may be shown from the several works of physicists. Several years ago Professor Young [2] examined the spectrum of the fire-fly and stated his important observations in the following form.

"The spectrum given by the light of the commom fire-fly of New Hampshire (*Photinus ?*) is perfectly continuous, without trace of lines either bright or dark. It extends from a little above Fraunhofer's line *C* in the scarlet to about *F* in the blue, gradually fading at the extremities. It is noticeable that *precisely this portion of the spectrum is composed of rays, which, while they more powerfully than any others affect the*

[1] Mosely: Notes by a Naturalist on H. M. S. Challenger, 1892, p. 512.

[2] C. A. Young: Spectrum of the Fire-fly. *Amer. Naturalist*, Vol. III, 1870, p. 615.

organs of vision, produce hardly any thermal or actinic effect. In other words, very little of the energy expended in the flash of the fire-fly is wasted. It is quite different with our artificial methods of illumination. In the case of an ordinary gaslight the best experiments show that not more than one or two per cent of the radiant energy consists of *visible rays*, the rest is either invisible heat or actinism ; that is to say, over ninety-eight per cent of the gas is wasted in producing rays that do not help in making objects visible."

Of Professor Langley and Mr. Very's more recent and well-known paper "On the Cheapest Form of Light,"[1] most of you are doubtless aware. As their observations are the most accurate extant on the physical properties of animal light, it will not be out of place to reproduce here at length the essential points of their conclusions, as well as some of their instructive statements on the concepts of radiant energy, which underly their experimental inquiries.

"We recall," says Professor Langley, "that in all industrial methods of producing light, there is involved an enormous waste, greatest in sources of low temperature like the candle, lamp, or even gas illumination where, as I have already shown, it ordinarily exceeds ninety-nine parts in the one hundred ; and least in sources of high temperature like the incandescent light and electric arc, where yet it is still immense and amounts, even under the most favorable conditions, to very much the larger part" (p. 97).

"It is now universally admitted that wherever there is light, there has been expenditure of heat in the production of radiation existing in and as the luminosity itself, since both are but forms of the same energy; but this visible radiant heat which is inevitably necessary is not to be considered as waste. The waste comes from the present necessity of expending a great deal of heat in invisible forms before reaching even the slightest visible result, while each increase of the light represents not only the small amount of heat directly concerned in the making

[1] S. P. Langley and F. W. Very : On the Cheapest Form of Light, from Studies at the Allegheny Observatory with Plates III, IV, and V. *The American Journal of Science*, Third Series, Vol. XL, No. 236, August, 1890.

of the light itself, but a new indirect expenditure in the production of invisible calorific rays. Our eyes recognize heat mainly as it is conveyed in certain rapid ethereal vibrations associated with high temperatures without passing through the intermediate low ones; so that if the vocal production of a short atmospheric vibration were subject to analogous conditions, a high note could never be produced until we had passed through the whole gamut, from the discontinuous sounds below the lowest bass, up successively through every lower note of the scale till the desired alto was reached.

"There are certain phenomena long investigated, yet little understood, and grouped under the general name of 'phosphorescent,' which form an apparent exception to this rule, especially where nature employs them in the living organism, for it seems very difficult to believe that the light of a fire-fly, for instance, is accompanied by a temperature of 2000° or more Fahr., which is what we should have to produce to gain it by our usual processes. That it is, however, not necessarily impossible, we may infer from the fact that we can by a known physical process produce a still more brilliant light without sensible heat, where we are yet sure that the temperature exceeds this. No sensible heat accompanies the fire-fly's light any more than need accompany that of the Geissler tube; but this might be the case in either instance, even though heat were there, owing to its minute quantity, which seems to defy direct investigation. It is usually *assumed* with apparent reason, that the insect's light is produced without the invisible heat that accompanies our ordinary processes, and this view is strengthened by study of the fire-fly's spectrum, which has been frequently observed to diminish more rapidly toward the red than that of ordinary flames. Nevertheless this, though a highly probable and reasonable assumption, remains assumption rather than proof, until we can measure with a sufficiently delicate apparatus, the heat which accompanies the light, and learn not only its quantity, but what is more important, its quality" (pp. 98, 99).

Under "Photometric Observations," the authors continue:

"The first impression in viewing the light of the *Pyrophorus noctilucus* through a spectroscope is that it consists essentially of a broad band in the green and yellow, while with precaution we see this extending into and beyond the borders of the blue and orange, but not very greatly farther, and these have been taken by previous observers as its absolute limits. No one appears to have experimentally and distinctly answered the question, "Would the light not extend farther were it bright enough to be seen?" nor has it been proved as clearly as might be desired that the result depends on the quality rather than the quantity of the light, or given conclusive evidence that if the light of the insect were as bright as that of the sun, it would not extend equally far on either side of the spectrum.

"It is impossible to increase the intrinsic brilliancy by any optical device, but if it be impossible to make the light of the insect as bright as that of the sun, it is, on the other hand, quite possible to make the light of the sun no brighter than that of the insect, and this would appear to be the first step in obtaining a definite proof that the apparently narrow limits of the insect's spectrum are due to the intrinsic quality of the light, and not to its feeble intensity. The only conclusive method of determining this would appear to be to balance the light from the insect with that of a definite portion of sunlight by any ordinary photometric device; and having taken this sunlight as nearly equal as possible to that of the insect, though certainly not greater, to let this determined quantity fall on the slit of a spectroscope at the same time with the light from the insect, two spectra being formed one over the other in the same field and at the same time" (pp. 103, 104).

After detailing a number of experiments, the authors state that "when spectra are formed from two *equal* lights, one from the sun, the other from the insect, the latter's spectrum terminates both at an upper and a lower limit, at which the solar light is still conspicuous. The conclusion follows that the insect spectrum is lacking in rays of red luminosity, and presumably in the infra-red rays, usually of relatively great heat, or that it seems probable that we have here *light without heat*, other than that heat which the luminosity itself comprises and which is but another name for the same energy" (p. 108).

Under "Thermal Observations" the authors proceed: "To give an idea of the amount of heat at our disposition for experiment, and of the actual minuteness of the radiation which proceeds from even the most luminous tropical insect, we may say that if that rate of radiation from a lamp-black surface 1 square cm. in area, which represents the amount of heat necessary to raise 1 gram of water to 1° centigrade, in 1 minute (*i.e.* one small calorie), be taken as unity, then the luminous radiation of the fire-fly's heat, per square cm., of exposed luminous surface, as we have found, is about 0.0004 calorie in 10 seconds, and the total luminous radiation from the most powerfully illuminating light spot of the insect (the abdominal one) will not exceed 0.00007 calorie in the same time. But a small portion of this could fall upon the bolometer, and that which actually reached it during the time (10 seconds) required for each observation was sufficient only to affect an ordinary mercurial thermometer having a bulb 1 cm. in diameter by rather less than 0.00000023, or by less than 1/400000 of one degree centigrade" (pp. 108, 109).

"Resuming, then, what we have said, we repeat that nature produces this cheapest light at about one four-hundredth part of the cost of the energy which is expended in the candle-flame, and at but an insignificant fraction of the cost of the electric light or the most economic light which has yet been devised; and that finally there seems to be no reason why we are forbidden to hope that we may yet discover a method (since such a one certainly exists and is in use on a small scale) of obtaining an enormously greater result than we now do from our present ordinary means for producing light" (p. 112).

The light emitted by the living organism differs very much in color in different animals, and even in the same animal at different periods; *green* has been noticed in the glow-worm, fire-flies, some brittle-stars, centipedes, and annelids; *blue* is seen in the Italian fire-fly; *blue and light-green* are the predominant colors exhibited by marine animals; the beautiful Girdle of Venus, some species of Salpa, and Cleodora appear *red;* Pavonaria and other gorgonids are *lilac;* and one hemiptera, Fulgora, is said to emit a *purple* light. One very remarkable

Appendicularia showed in one individual first *red*, then *blue*, and finally *green*.[1] This remarkable property seems to be possessed by other tunicates, for Huxley[2] states in his well-known paper on Pyrosoma, quoting Péron, that Pyrosoma exhibited movements of alternate contraction and dilatation at regular intervals; and that each contraction was accompanied by the development of a luminosity, which, when at its brightest, was *red*, but in dying away passed through shades of *orange*, *green*, and *blue*. Newport[3] also noticed a change in the color of light emitted by the glow-worm at the end of the season from that at the beginning. I have learned in the study of several species of fire-flies, in the neighborhood of Woods Holl laboratory, to distinguish them at a distance by the color of their light, which, though slight, is still quite characteristic of the species.

The difference in color, when exhibited by different organisms, is probably due to some slight chemical differences in the light-giving substance. It may be supposed that under the influence of oxygen, the molecules of the given photogenic substance are set in vibration, the rate of vibration depending on and being characteristic of the particular species. And in those cases where a series of colors are displayed in succession by the one and the same organism, it may be supposed to be due to either of two causes: (1) the same photogenic substance is agitated with different degrees of frequencies at different periods in the life of the organism, or (2) a series of photogenic substances are produced, each one of the series representing a stage in the chemical metamorphosis of the substance. Without some definite chemical knowledge on the nature of such photogenic substances, however, it is useless to make any conjecture at present.

Nor is it easy to offer any plausible explanation as to the use of such light to the organism, which will apply with equal force to all cases. We may say this much, however, that if heat inci-

[1] The above is taken from W. E. Hoyle's article Phosphorescence, in the *Encyclopædia Brittanica*, Vol. XVIII, 1885.

[2] Huxley: On the Anatomy and Development of Pyrosoma. *Phil. Trans.*, 1859.

[3] Newport: On the Natural History of Glow-worms. *Proc. Lin. Soc.*, Vol. I, 1857.

dentally produced at first as a result of some necessary chemical changes in the body may be utilized in the course of the race history of an organism (as among birds which use heat evolved by the metabolism of their tissue for the process of incubation), it is equally conceivable that light incidentally produced as the result of a necessary combustive process of life may eventually be utilized in the race history of some species, and thus that which is an end in one organism may become the means to a remoter end in another organism. The mere fact that in some animals the light is of no apparent use to them is no reason to doubt that it may be of some use to others, in which the production of light becomes the end and purpose of some definite structure, and is even brought in connection with the mechanism of the will.

While the production of light may be regarded as belonging to the same ultimate cause as that of heat, the proximate cause of the luminosity in the animal kingdom may be due to a variety of secondary circumstances.

Thus (1) an organism may appear brilliant in the dark, owing to the presence of luminous bacteria in the tissue.[1] In such a case, the luminosity of the organism may be considered as a pathological phenomenon.

In another instance (2) the organism may appear luminous also on account of the luminous bacteria which live in a symbiotic fashion in the tissue of the organism, but this cannot be called a disease, as the animal suffers no bad consequence, and may even be benefited by it.[2]

In still another case (3) transparent pelagic organisms like some crustacea may appear phosphorescent from containing in their stomachs phosphorescent food, which shines through the body of the organism. In a case like this their excrement is also phosphorescent.[3]

[1] See Giard: Sur l'infection phosphoresc. des Talitres et autres crustacées. *Compt. Rend.*, Sept. 23, 1889, p. 503. Peter Schmidt: On the Luminosity of Midges (*Chironomus*). *Zool. Jahrb. Abth. f. Syst. Geog. und Biologie*, Bd. VIII, Heft I, 1894. *Ann. and Mag of Nat. Hist.*, Vol. XV, 1895 (translated by Austen).

[2] R. Dubois: Sur le rôle de la symbiose chez certains animaux marins lumineux [Pelagia et Pholas]. *Compt. Rend.*, Tome CVII, 1888, p. 502.

[3] H. N. Moseley: Notes of a Naturalist, p. 498.

In the truly phosphorescent organism the luminosity is due to the metabolism of the definite tissue-cells, and the subsequent oxidation of the metabolic product, which results in the emission of light.

There can be no doubt that the majority of luminous organisms belong to this type. In some, certain cells of the body acquire the light-producing property at a certain stage of development; in others, the organisms are luminous from the beginning of their life history. Thus Alexander Agassiz[1] observes "that the phosphorescence is equally brilliant in the egg of Ctenophoræ as in the adults, even in stages in which the masses of segmentation can still be counted. The whole embryonic mass becomes brilliantly phosphorescent when the least shock is given to the jar in which the eggs are kept."

Dubois[2] also states that in *Lampyris noctiluca* the ova taken from the ovaries and carefully washed after removal were still luminous, the development of the light being in direct relation with the degree of intraovarian development of the ova. The photogenic power in such an egg, as in many luminous protozoa, is exercised without the aid of trachea, nerves, or special anatomical elements, showing that while these elements may facilitate and even enhance for the time being the effect of luminosity, they are not to be considered thereby essential to the process of light production.

Phosphorescence is best seen in the ordinary fire-fly. If you examine the luminous cell of the common fire-fly (*Photuris pennsylvanica*), you will find it filled with peculiar yellowish-white granules, the whole cell reminding one of some actively secreting gland. These granules, by combining with oxygen brought in through the trachea and tracheal "capillaries," which closely invest the cells from all sides, give out light. It is a process of combustion which, instead of giving out heat, gives out light. These granules are the products of metabolism, the result of "secretion" process, due to the

[1] A. Agassiz: Embryology of the Ctenophoræ. *Mem. Amer. Acad. of Arts and Sciences*, Vol. X, No. IV. Cambridge, Mass., 1874.

[2] R. Dubois: De la fonction photogénique dans les œufs du lampyre. *Bull. Soc. Zoöl. France*, XII, 1887, p. 137.

decomposition of the living substance of the cell; but instead of being thrown out of the body, like some other products of secretion, they are consumed *in situ* by combining with oxygen brought in from without.

The fact that the granules themselves are dead is shown by taking the luminous organ from the organism and crushing it on the slide, thus depriving it of all traces of vitality; yet the light continues to come out, in fact it becomes more luminous the greater the exposure to air.

The mode by which each luminous cell is aërated by the tracheal "capillaries" is of considerable interest. The "capillaries" are the ultimate branches of the respiratory apparatus, and start from the ultimate branches of the tracheal tube, somewhat in a similar manner as the tentacles do from the body of a hydra. If one imagines these "capillaries" are spread around the photogenic cell in the same manner as the hydra spreads its tentacles around an organism much larger than itself, which it has captured for food, he may get a fair idea of the relation of the aërating apparatus to the light-producing cell.

The size of the luminous cell being comparatively large, more than one bunch of hydriform "capillaries" is found distributed over the surface of each luminous cell. The substance of the "capillaries" seems to have a remarkable affinity for oxygen, and it is, no doubt, through this mechanism that the oxygen of the inspired air is quickly separated, and just as quickly applied for the combustion of the photogenic material in the periphery of the cell.

As to the chemical nature of this material little is known; but it is a secretion of fatty nature, which oxidizes readily in alkaline media. Phosphorus has nothing to do with the phenomenon.

The animal has control of the production of light through its respiratory mechanism, not directly upon the luminous cell, although nerves may have indirect influence upon the general metabolism of the cell. When more oxygen is sent with the air, the illumination is greater; when the air is withheld, there is less light, or even a complete darkness, just as the dull red coal may be ignited so as to emit a white light by a steady application of fresh air upon it by the action of the bellows.

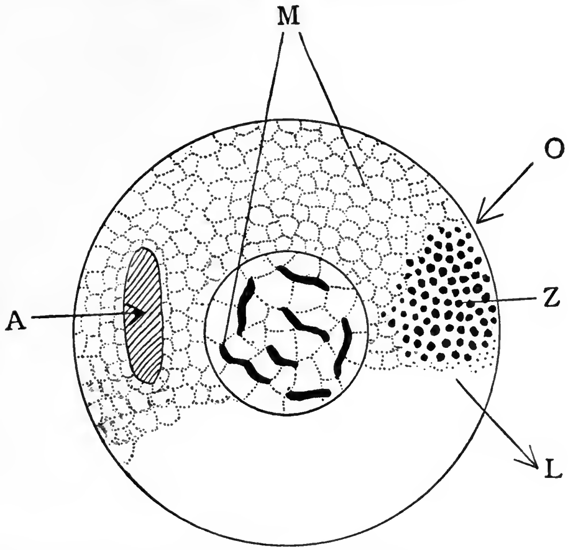
The fact that the illumination of the cell is due to the action of oxygen may be shown in a simple way by putting the slide on which the luminous organ has been crushed, and the photogenic material spread out, into a jar containing carbon dioxide. The light disappears almost instantly; but if the same slide be placed in a jar containing oxygen, or simply exposed to air, the light comes back, and lasts as long as the luminous material, a certain amount of moisture, and other necessary conditions are present.

This process can be repeated several times, showing conclusively that the light-giving material itself is quite independent of cell-life, although it owes its existence primarily to the life activity of the cell as a whole.

The luminous phenomenon, wherever it occurs, is apparently carried on by essentially the same process throughout the animal kingdom. In air-breathing organisms, such as the fire-fly, the product of cell metabolism is oxidized *in situ* by the oxygen of the inspired air. In some marine organisms the secretion is often thrown out in the form of liquid from the gland to the surrounding medium, and the oxidation is accomplished by the oxygen dissolved in the sea water. In luminous Salpa the photogenic granules formed in the blood-corpuscles are oxidized by the oxygen dissolved in the blood plasma.

Perhaps I can summarize the preceding, and make my point more intelligible by the help of a diagram.

We have seen that the essential bases for the luminous phenomena of the living organism consist (1) in the production of a certain chemical substance in the cell, which recalls to our mind the well-known series of phenomena in the process of secretion; and (2) the oxidation of this substance by the oxygen brought in from without, and thus making the cell a new center of disturbance to the surrounding ether.



LIVING CONSTITUENTS OF THE CELL.

M Protoplasm { (a) Cytoplasm. (b) Chromosome.

O Oxygen, acting on the photogenic granules.

L Light, emanating from the cell, as the result of oxidation.

NON-LIVING CONSTITUENTS OF THE CELL.

{ (a) *Food* (*A*). (b) *Photogenic granules* (*Z*).

The food-substance, which I represent, for the sake of convenience, by the block (*A*) in the accompanying diagram, enters the cell boundary, and becomes eventually assimilated into the protoplasm (*M*); the complex living substance, or protoplasm, becomes disintegrated into a number of granules (*Z*) which are no longer "living," and which may be regarded as refuse of life. The definite chemical molecules which constitute these granules combine with oxygen (*O*), and the molecular agitation, which accompanies the chemical process of combustion, sets the surrounding ether into a state of vibration (*L*), which has a powerful luminous effect on us, but little or no thermal effect.

Thus, the life of the luminous cell, like that of any other cell, begins with the physical and ends with the physical. We know the beginning (*A*); and we also know the termination (*L*). The unknown territory in the middle (*M*) is what we call the protoplasm, or the matter in the living state.

There is one suggestion of some importance which flows from this.

That most living matter needs oxygen for the maintenance of life is a well-established fact, but in what precise manner this oxygen is ultimately used in the organism, is a question to which we can give hardly any satisfactory answer at present.

In the luminous cell of the fire-fly, in which the mechanism of oxygenation is carried to its highest perfection, it is comparatively easy to trace the path of oxygen, and how it is used in the living cell. *The oxygen here simply combines with the dead substance prepared in the cell.* The value of oxygen to the luminous function of the organism lies in its ability to combine with the dead substance produced by the activity of the living. Is it possible that the relation of oxygen to life in general is of a similar nature? Does the value of oxygen to life lie primarily in its ability to combine with the dead substances, which exist side by side with the living, in all cells? The hæmoglobin is a complex iron compound found in the red blood-corpuscle. Oxygen loosely combines with this compound and forms oxy-hæmoglobin. The oxygen in this new compound is given up in the tissue through which the blood circulates, and the compound returns back to the original hæmoglobin, which, coming back to the respiratory organ, combines again with the free oxygen, and begins the rôle of oxygen-carrier again. Here, again, the substance in the cell which combines with the oxygen is not the living substance, but the dead material formed by the activity of the cell. Professor Loeb suggests that it is possible that the relation of oxygen to life may be of this nature in all cases.

It may be that in the luminous cell of the fire-fly the method of oxidation is carried out with a highly specialized apparatus, and the result of oxidation of the dead material conveyed in such a form as to affect the most delicate of our sense-organs, and that the relation of oxygen to the life of the cell in general is thus revealed here with simplicity and clearness unparalleled in the whole series of vital activities. At any rate, this aspect of the question may not be devoid of interest when taken in connection with the fundamental problem of the relation of oxygen to living substance, or respiration, in which, some have even maintained, lies hidden the whole mystery of life.

EIGHTH LECTURE.

THE PRIMARY SEGMENTATION OF THE VERTEBRATE HEAD.

WILLIAM A. LOCY.

(LAKE FOREST, ILL.)

THE vertebrate head is the most complex piece of animal architecture with which anatomists have to deal. It has been produced by gradual modifications of a simpler basis, and differentiation has been carried farther in it than in any other part of the animal. It represents, therefore, the widest departure from archetypal conditions.

Its complex structure is correlated with the highest grade of functions. The cranial sense-organs and the brain exhibit the highest manifestations of vital activity to be found in the whole range of living structures. The cranial sense-organs serve to bring the organism into relation with the external world, and the brain, besides being concerned with perception and general mental life, contains nerve-centers for the coördination of the vital actions of the body. The structure and development of the vertebrate head is therefore a topic of unusual interest and importance in comparative anatomy.

In their efforts to understand the head, morphologists and physiologists have made use of every available means of research; observations on the minute structure have been supplemented by studies in embryological development and physiological experimentation. The whole work has been carried on from the standpoint of comparative anatomy. The results have not been just what might have been expected. They have not led to the solution of the fundamental questions, but have served rather to open the field and reveal its extent and complicated nature. A research once begun leads out in all directions into the unknown, and a crop of new problems springs up in the path of the original investigator. It is encouraging to biologists to know that every research serves to enlarge the field of their activity; the conquered territory affords points of vantage from which the horizon is enlarged. Thus the work of morphologists and physiologists on the head, although not giving a complete solution to the problems undertaken, has brought us larger views and more interesting and suggestive lines of inquiry.

Out of the great group of subjects connected with the morphology of the head, I have chosen one that relates to the primitive segmented condition. If we propound the question, What was the rudimentary condition of the vertebrate head? we shall find it may be partly answered in the light of modern research as follows: It was originally composed of a series of similar segments that were structurally like those that compose the trunk. A mental picture of this rudimentary condition may be formed by thinking of the broad cephalic plate (or rudimentary head) of very early embryonic stages as divided by transverse constrictions into ridges and furrows that pass backward from the head into the trunk, and give the whole embryo a jointed structure similar to that of an articulated animal. The segments or folds do not cross the median plane, and are therefore in pairs. From this simple condition the complex head has arisen by differentiation and specialization. It follows, of course, that the distinction between head-region and trunk-region is one of degree of differentiation and not of kind.

The head is least modified in the youngest embryos, and if we begin our observations with the earliest stages its transformations may be traced by observing successively older embryos. The modifications which the head has undergone have been brought about gradually, and are so comprehensive in their range that if we could know their complete history, even in one animal, we should have a key to the leading questions of vertebrate descent. But there are so many causes tending to modify the course of development, that we cannot depend on the steps of ancestral history being repeated in a complete and orderly way in any animal form, and our observations give us only circumstantial evidence from which a balance of probabilities must be struck to determine what is ancestral and what is secondarily acquired. The chain of evidence is incomplete, and must always be supplemented by a certain amount of inference, but it has not been fully recognized in the practical study of embryological development that the shortest intervals of time may be very important in keeping the connection. Coherency of history must be preserved. The difficulty of doing so is greatly increased by the fact that the new is made to proceed out of the old, and frequently one organ insidiously takes the place of an earlier formed one. I am glad of the opportunity to say, in this company of investigators and students who are preparing for independent research in biology, that too great stress cannot be laid on the desirability of having a more complete series of stages for study. The traditional method has been to study one stage, and then another "a little older," and fill in the gap with inferences. This has proved to be inadequate and misleading. It is now required that we shall have stages near enough to trace the history of the transitory as well as the permanent organs; embryologists are just beginning to realize how transitory some organs are. I have recently had occasion to examine a set of embryonic structures in the chick, which do not apparently last more than an hour or two in the course of development, but which are, nevertheless, clearly defined for that period and then fade away. In this particular case the agreement of two observers, even as to the presence of these organs, would depend on their having stages of identically, not approximately, the same period of development. A wider recognition of the existence of such conditions would give us fewer controversies and less biological mythology.

Above, it was stated that the vertebrate head is primitively segmented, and it is manifestly an interesting problem to determine the number, the nature, and the transformations of the segments that have entered into the composition of the head. The individual segments are called metameres, or somites, and the jointed condition is designated "metamerism of the head." Under that title the question has recently received much attention. It is not a new question, having been started at the beginning of this century, but there has been a revived interest in it on account of new discoveries. It was the most prominently discussed question before the Anatomical Society of Germany, at their meeting in Vienna, in 1892. There were important papers on the subject by some of the foremost anatomists, — Froriep, Kupffer, Hatscheck, Rabl, Killian, — all followed by discussion, and the question of metamerism of the head received there a consideration worthy of its importance. There have been new developments since that time, tending to modify some of the conclusions reached in that learned body, and the subject is, on account of its freshness, a particularly good one to present here.

The presence in the head of such segmental structures as cranial nerves, branchial clefts, of the adult and embryonic stages, the so-called head cavities and neural segments, have been sufficient evidence to support the general proposition that the vertebrate head is segmented in its unmodified condition. But there has been no agreement as to the number, nature, or transformations of these segments, nor as to their anterior limit. In fact, the fore-brain has generally been regarded as not included in the segmented area.

Segmental folds have been observed in the hind-brain of embryos of different animals since 1828, so there has been no question as to the segmented condition of the posterior part of the brain, but, so far as the evidence (except the very latest) goes, the segments seem to vanish in the region of the fore-brain, and the general interpretation has been that the fore-brain is non-metameric. The two anterior pairs of nerves coming from the fore-brain — olfactory and optic — have also until very recently been placed, by common consent, in a different category from the other cranial nerves. Moreover, the head has been considered, by some of the most careful students of our time, to be derived from an unsegmented ancestral rudiment found in an enigmatical larval form of the annelids. All this gave rise to the assumption that the brain of invertebrates and vertebrates contained an unsegmented anterior part, and the question, How far forward does the segmentation extend? is a very important one.

The evidence to elucidate this point has been accumulating, and I think we are now in a position to answer that fundamental question. Already the olfactory nerves have been shown to have a similar history to the cranial nerves, and, to all appearances, the optic nerves are soon to be included with the others. The Director of this laboratory has recently shown conclusively that the head of annelids is metameric throughout. The cerebral ganglion or brain of these animals is segmented in the same manner as the ventral nerve-cord, and consequently there is no non-metameric part of the nervous system, as has been so long assumed. This must necessarily change the views regarding the ancestral derivation of the vertebrate head. Waters, Zimmerman, and others have shown the existence of segments in the fore-brain of vertebrates, and further evidence on that point will be brought out in this lecture.

The recent endeavors to solve the problem of metamerism of the head are based on observations on cranial nerves and branchial clefts, mesoblastic head cavities and neural segments. These are the cephalic structures that exhibit segmental arrangement, and we must depend upon them for evidence. It is an open question to which of these the most importance is to be attached. The first-mentioned basis, namely, cranial nerves and branchial clefts, is the least favorable, as it involves too much conjecture. Dr. Strong, of Columbia University, has shown that the cranial nerves do not appear in the positions they come to occupy, and McClure has stated the case against the cranial nerves as follows: "We have positive proof that the degeneration of certain branches has taken place. This being the case, we have every reason to assume that whole segmental nerves may have once existed, which have completely degenerated, leaving no trace whatever of their previous existence. If such be the case, the segments originally connected with these degenerated nerves must necessarily be overlooked, if the existing nerves are made use of as a means of determining the original number of segments.

"Furthermore, the vagrant changes in the position of some of the cranial nerves must necessarily cause confusion. For example, take the sixth nerve, which in the frog and tadpole stages is situated between the first and second roots of the ninth nerve (given on the authority of Dr. Strong), a position somewhat posterior to its place of origin. This remarkable shifting clearly shows not only what great changes in position the cranial nerves are capable of undergoing, but it also goes to prove that we can find no reliable means of determining the primitive segments by means of their connection with the exit of the existing cranial nerves. Beard, in taking up this problem, made use of an important series of sense-organs for which he proposed the name 'branchial sense-organs,' from their development from thickenings of the epiblast over each branchial cleft. The dorsal branches of certain cranial nerves fuse with these epiblastic thickenings; the superficial part of the thickening gives rise to a branchial sense-organ, while the deeper portion becomes the ganglion of the dorsal root of the cranial nerve. This close relation which exists between the dorsal branches of the cranial nerves and their corresponding sense-organs is undoubtedly of segmental character. But this line of research is beset by a great difficulty, namely, that the degeneration of certain sense-organs would, in time, involve the degeneration of their corresponding cranial nerves, and such degeneration has taken place, in part or in whole, leaving in doubt the primitive segments with which they were connected."

The mesoblastic head-cavities and neural segments are both more important clues to the metamerism of the head. The mesoblastic head-cavities are called myotomes, and embody the muscle rudiments, while the neural segments represent the joints of the nervous system. Muscle and nerve are, physiologically, so fundamentally related that we should naturally expect some close correspondence between muscle segments and neural segments, and metamerism of the head should be studied in the light of observations on both sets of structures.

Balfour first studied the segmental divisions of the mesoblast in the head of elasmobranch fishes, and, in 1874, identified by this means eight head somites. He also expressed the conviction that there were primitively a larger number of segments, but, owing to extreme modifications of the head-region, they are no longer clearly represented.

From this time onwards, the myotomes became a great favorite with morphologists in elucidating the problem of head segmentation. They seemed, so far as the evidence went, to embody the most direct survivals of the original segmentation, and therefore to be the most promising line along which to work out the problem. Van Wijhe's researches, published about 1882, have been taken as the standard ones for reference; he identified nine head somites moulded in the mesoblast of the head. This line of investigation received a great stimulus in 1890, from the work of Dohrn, who discovered eighteen or nineteen myotomes in the head of torpedo embryos. In 1892 Killian substantiated his discoveries and reduced the enumeration by one. It appears, therefore, that there is a larger number of head somites than was at first supposed.

The neural segments are comparatively recent in their claims to attention as bearing evidence to the original segmentation of the head, and their importance in this connection has not been fully appreciated. Their early history has recently been made known,[1] and this shows them in a new light. The neural segments are the first to appear, and are less subject to modifications in the early stages than the muscle segments of the head. The large number of myotomes described by Dohrn and Killian are transitory, and after a very brief existence they become reduced by fusion, or absorption, or both, to the nine head-cavities of Van Wijhe. But the neural segments make their appearance very early and preserve their original number and characteristics for a considerably longer period. It has been assumed that the muscle segments are primary and that the neural segments are secondarily moulded over them; but, as we shall see, this position cannot be sustained in the light of recent observations, and it is timely to ask which set of segmental structures affords the most reliable evidence as to the primitive number of brain segments.

[1] Locy: Metameric Segmentation in Medullary Folds and Embryonic Rim. *Anat. Anz.*, Bd. IX, No. 13, 1894; also *Journ. Morph.*, Vol. XI, No. 3.

I have said that the metamerism of the head should be investigated in the light of work done on both myotomes and neural segments, but here I can present only one side. The case for the myotomes has been so completely presented by Dohrn, Killian, and others that I waive a consideration of that side of the question, and dwell on the history of the neural segments and speak of the new observations on them.

The neural segments were observed in the hind-brain of embryo chicks by Von Baer as long ago as 1828. They have been observed and commented upon by many anatomists since that time. In 1850 Dursy made the important suggestion that the neural segments are genetically related to the cranial nerves, but he had no direct evidence of this. To Béraneck belongs the credit of having first demonstrated, in 1884, that there is a definite relation between neural segments and certain cranial nerves. This was the first substantial basis towards establishing their segmental importance. Orr, '87, McClure, '90, and Waters, '92, followed this pioneer work, demonstrating the definite relation[1] of the nerves of the hind-brain to specific neuromeres. McClure showed also that the entire neural tube is divided into similar segments, and Waters gave particular attention to the fore- and mid-brain. He found in the lizard evidence of three somites in the fore-brain, making a total of eleven somites in the entire brain-region.

In Europe Froriep, Kupffer, Rabl, Hoffmann, Zimmerman, and others have made recent contributions to the knowledge of these neural segments. In 1892 Froriep described anew the neural segments and attached no particular importance to them. He expressed the conclusion that the neural segments are secondarily moulded over the segmental divisions of the mesoblast. The latter, in common with most other writers, he regards as primary. I hope to show you before the conclusion of this lecture that the position cannot be sustained.

Let us now see what may be learned regarding the primitive segments of the head by the examination of young embryos.

[1] I prefer to omit in this general lecture the question of the relationship of particular cranial nerves to particular neural segments, which is of so great interest and importance to the morphologist.

In choosing an advantageous animal for observation, we should take a vertebrate that has undergone relatively few modifications. Of course, any living animal is very far removed from the ancestral type, but we should expect to find the closest approach to ancestral conditions in the simplest ones. The sharks present many generalized features and we may as well begin with them.

It is to be understood that I am responsible for the observations that follow, as they have not, as yet, been substantiated by any other observer. The careful examination of an elasmobranch embryo in an early stage of development shows the existence of segmental folds that extend from the extreme

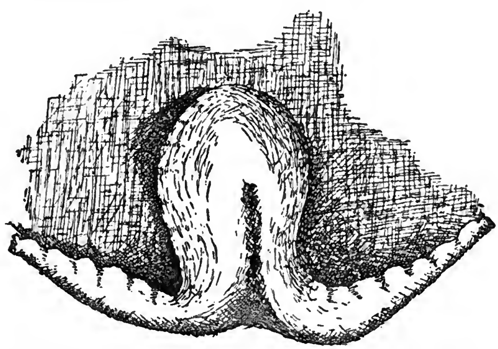


FIG. 1. — Very young embryo of Acanthias showing primitive segments.

anterior end to the posterior limit of the embryo. Fig. 1 represents such an embryo. The specimen from which the sketch was made had attained a length of 1.1 mm. The axial part of the embryo is established; its anterior end is rounded and slightly broader than the rest of the embryo. There are eight pairs of segments in the axial embryo, and they extend beyond into the blastodermic rim. If these segmental folds occurred only in isolated cases, or in a single embryonic stage, we should attach no especial significance to them, but they are present in all normal specimens, and their history shows their segmental importance. Once established, they may be traced onwards in unbroken continuity and finally identified with the neuromeres described by Orr, McClure, and others. There are three or four pairs of mesoblastic divisions in this stage that occupy a limited area in the narrow part of the embryo, but the segmental folds are comprehensive in extent and cannot depend on these few protovertebræ.

The examination of a slightly older embryo, Fig. 2, gives a

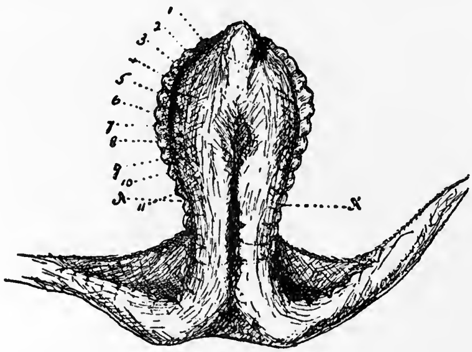


FIG. 2. — Young embryo of Acanthias showing primitive segments. Those numbered 1–11 lie in front of the point of origin of the vagus nerve.

similar picture. The segments are a little better developed, and the broad head-region is roughly marked off from the more slender trunk-region. The segments extend along the margin in pairs. As in the former case, they extend beyond the limit of the axial embryo into the embryonic rim. There are eleven pairs in the broadly expanded head end. It may be determined by tracing them into later stages that the eleventh neuromere is just in front of the place of origin of the front root of the vagus nerve.

It is obvious that this young animal that is to be hatched from the egg as a vertebrate is now an invertebrate. It exhibits an arthromeric condition similar to that in animals of the articulated group. The segments, although faintly expressed, are definite in number and arrangement, and the inference to be drawn from their presence is clear. As Dr. Whitman has said: "This is a stage through which every vertebrate passes on its way from the egg to the adult, a stage in which the fish, the amphibian, the reptile, the bird, the beast, and man find a common level, and in which every title to superior rank lies in unexpressed potentialities. But more than this; for it is here that the vertebrate is an invertebrate and stands beside its prototype, the segmented worm. On the same metropolitan plane the lobster, the crab, the insect, in short all the members of the great arthropod group, meet and acknowledge their community of descent. Thus the great branches of the genealogical tree represented in the larger types first defined by Cuvier converge and meet in a common trunk which bears the deep and enduring mark of metamerism."

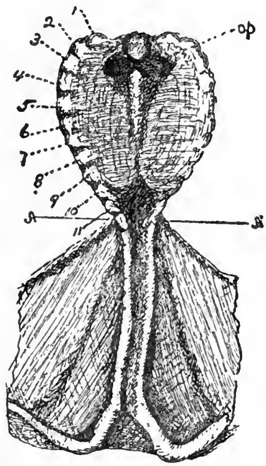


FIG. 3. — Older embryo showing metameric segments in the head-plate. The neural folds of the head are nearly in the horizontal plane. *op*, beginning of the optic vesicle.

Fig. 3 shows an older embryo with a slender trunk and broadly expanded head. The optic vesicles (*op*) have made their appearance on the head-plate. The neural segments are well shown on the left-hand margin of the cephalic plate.

Fig. 4 shows a still older embryo in which the neural folds of the head have grown upwards to form an open neural groove.

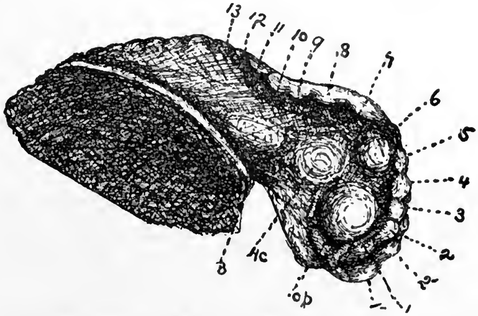


FIG. 4. — Embryo with open neural groove. 1–13 metameres of the neural folds. *op*, primary optic vesicle. *hc*, head-cavity.

The embryo is viewed obliquely from the right side. The rudiments of several organs — optic vesicles, branchial pouch, etc. — have appeared upon the lateral walls of the head. Directing our attention to the margin of the nearest neural fold, we note that it is clearly segmented throughout the head-region, and backwards into the trunk to the point where, in the figure, it disappears behind the yolk. The metameres extend, in reality, to the posterior limit of the body.

The next stage to be considered, Fig. 5, is immediately after

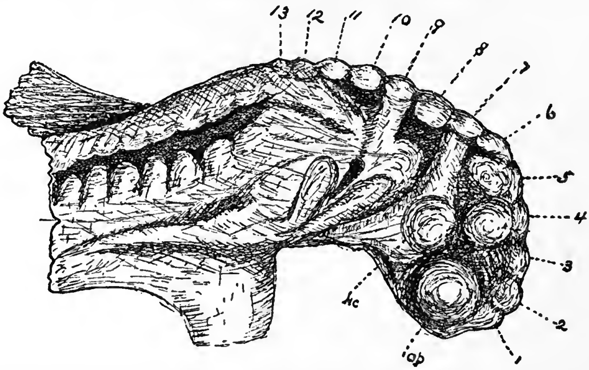


Fig. 5. — Head of embryo of Acanthias after closure of the neural groove but before the formation of the auditory vesicle. Reference marks as in the previous figure.

the closure of the neural groove and before the auditory vesicle has made its appearance. Certain anatomical landmarks of the head-region have become established, and it is now possible to determine the relation of the neural segments to other cephalic structures.

It is to be noted that the metameres of the fore- and mid-brain are still visible from surface views, and almost immediately become indistinguishable in these regions, but continue to be well defined in the hind-brain. There are five segments well shown in the combined fore- and mid-brains. Three of these probably belong to the fore-brain and two to the mid-brain. All the embryos so far described exhibit the segmental folds to the anterior end of the head, and a definite answer is returned by these observations to the fundamental question already proposed: How far forward does the segmentation extend? In view of the facts, we are justified in concluding that the extreme anterior end of the vertebrate brain still bears the marks of primitive segmentation. This, as Dr. Whitman has shown, is also the case with the invertebrates.

In Fig. 6, the auditory vesicle is formed. The neural segments of the fore- and mid-brains are no longer discernible

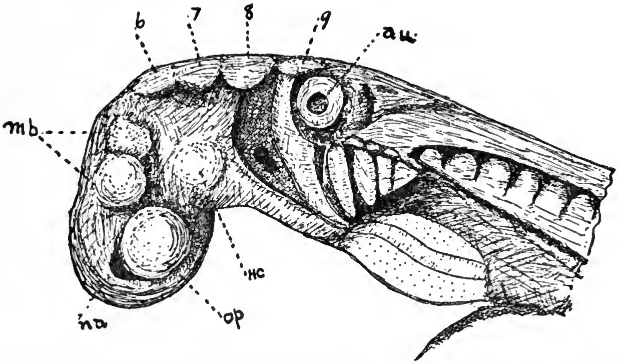


FIG. 6. — Head of embryo after the formation of the auditory vesicle, the first five head segments no longer distinguishable. *au*, auditory vesicle. *na*, nasal epithelium. *mb*, mid-brain.

from surface view, but those of the hind-brain, beginning with No. 6, are clearly seen. The neuromeres of that region are now in contact in the median plane; soon, by the lateral growth of the upper brain wall, they become separated as shown in Fig. 7. This is the stage in which neural segments have been heretofore described. They have been designated neuromeres. The

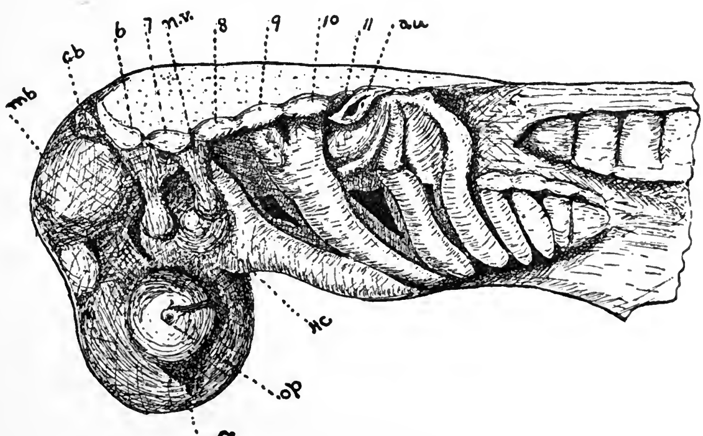


FIG. 7. — Head of embryo somewhat older than the one in Fig. 6. *nv*, beginning of the fifth nerve. Other reference marks as before.

cranial nerves have begun to develop and show definite relations with some of the neuromeres of the hind-brain. For example, as is best shown in Fig. 7, the fifth nerve is connected with the first and second neuromeres of the hind-brain, that is, with the segments Nos. 6 and 7. The eighth neuromere has no nerve connection; the seventh and eighth nerves are connected with the ninth and tenth neuromeres; the ninth nerve with the eleventh neuromere, and the front root of the vagus is connected with the twelfth segment.

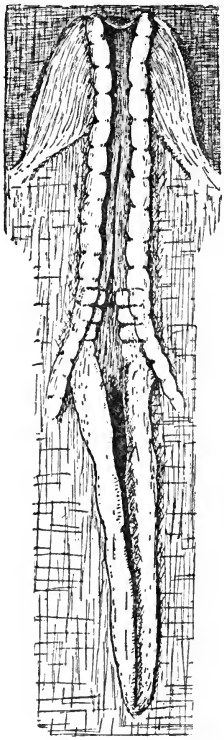


FIG. 8. — Embryo of chick, with open neural groove and three well-marked mesoblastic somites. The neural folds are segmented throughout their extent.

The evidence of a primitive head segmentation, which is so well preserved in these animals, is by no means exceptional, as may be determined by examining the embryos of other animals. They are present at least in correspondingly young stages of birds and amphibia, and this considerable range indicates they are a fundamental characteristic.

In the very young chick, I have repeatedly examined them in living specimens. They are to be faintly seen as early as the twelfth to the fifteenth hour of incubation; and from that time onwards they are ever present till they are obliterated by transformations in the brain. In the earlier stages in which I have observed them there are only three pairs, and they apparently increase in number by backward growth. Fig. 8 shows the appearance of these segments in a chick embryo while the neural groove is open. The segments extend from the anterior limit of the head as far back as the neural folds are established; there are here four protovertebræ, but lying in front of them and entirely distinct from them are eleven pairs of the primitive neural segments.

These segments have also been studied in living embryos of several amphibia in stages with an open neural groove. They have also been identified in the early stages of the newt, the frog, and the torpedo.

The neural segments have now been shown to occur in the very early stages of a number of animals. The fact of their presence in these early stages once established, they assume new importance. They have a too definite history to admit of being set aside as mere beadings or undulations of no metameric significance. The fact has to be confronted that these neural segments are the early stages of the neuromeres, whose characteristics have been determined by a number of observers. So long as the neuromeres are supposed to be moulded over the mesoblastic somites, they can have no particular importance in the problem of head segmentation, but that view of the neuromeres is an assumption made without a knowledge of their early history. This early history, now made known, places them in a new light, and, taken all together, the neural segments furnish, I think, a more satisfactory basis for interpretation of metamerism of the head than we have had before.

There is one question regarding the validity of these segments that must be disposed of before we can proceed further. All investigators know that appearances simulating regular structures may be produced by the reagents used in preparing material for study ; and the question comes to us, Are not these segments artifacts produced by the action of chemicals? Too great precaution cannot be taken in sifting this matter to the bottom. The large number of specimens studied as a basis for the facts already given were prepared by a variety of methods. They were treated with reagents well known to morphologists, such as picro-sulphuric acid, picro-nitric, Flemming's solution, Davidoff's corrosive-acetic, chromic acid with a trace of osmic, corrosive sublimate removed with iodine ; and in all cases the segments have been distinguishable, not in patches but in such condition as to admit of being counted, and there has been uniformly the same number of segments in the head-region. It is not reasonable to assume that the different reagents would all produce the same effect.

The history of these segments, in Acanthias and the chick, has been followed very carefully, and the earliest formed ones have been traced without a break into later stages and identified with the neuromeres. If, therefore, the segments of the open neural groove stage are artifacts, it may with equal force be claimed that the so-called neuromeres, which are their later stages, are also artificially produced.

It should also be borne in mind that similar segments exist in correspondingly early stages in Amblystoma, Rana palustris, the newt, and the chick, which indicates that they are not confined to isolated cases but are a fundamental feature of vertebrate development.

The most satisfactory indication of their true nature is found by observing living material before it has been brought into contact with any reagent. Fortunately, the chick offers at all times a source where we can get living embryonic material of any desired age. These segments have been repeatedly observed in living chick embryos of the eighteenth to twenty-second hour of incubation, and have been treated with reagents while they were actually under observation. The effect of the addition of picro-sulphuric acid is to render, immediately, the walls of the neural groove opaque and more clearly defined, but not to affect the number or arrangement of the segments. The same segments have also been studied in living embryos of Amblystoma. These facts are conclusive; if the segments exist in living embryos, they are veritable anatomical structures.

Two points of fundamental importance may now be regarded as established: (1) that the neural segments are present in extremely early stages of vertebrates where they have not heretofore been recognized, and (2) that they are true anatomical structures and not artifacts. The question still remains, Do they furnish the best or even a good clue to the number of segments in the primitive brain? If so, they must be shown to be equally important in this direction with myotomes, branchiæ, and cranial nerves.

In estimating the claims of these various forms of segmental divisions to rank as the primitive, the time of their respective appearance in the developmental history will be significant.

On this point I wish to observe that in all the forms studied, embracing representatives of birds, amphibia, and selachians, the neural segments are among the first anatomical structures to be established; before the vestiges of any organs have appeared, the embryo is divided throughout its length into similar segments. These metameric divisions, therefore, antedate myotomes, branchiæ, cranial nerves, or any other structures that exhibit metamerism. They persist through the early stages of development, and become definitely related to segmental nerves and segmental sense-organs. In the light of their early appearance and their history, I think we are justified in saying they are the most satisfactory traces of primitive metamerism that are preserved in the group of vertebrates.

It should also be observed that the entire embryo is segmented, and the term "metamerism of the head" should be understood to signify merely regional metamerism, and not a different kind of segmental division from that occurring in the rest of the embryo.

The next point to be noted with regard to these segments is that they are formed independently of mesodermic influence. I have shown that the neural segments appear much earlier than those of the mesoderm, and that they extend throughout the embryo; when, however, the protovertebræ appear they are localized, and are formed backwards and forwards from the point of their first appearance. But the final appeal must be made to sections. A careful study of sections of shark and chick embryos shows that the mesoblast is not divided into protovertebræ in the head, even after that region is completely segmented. In the sharks also, the neural folds that are so evidently segmented, are at first wing-like expansions from the body, and during this stage no mesoblast enters into them. Therefore, the neural segments cannot depend upon the segmental folds in the mesoblast. The combined facts place the neural segments on a good basis for independent consideration as survivals of primitive segmentation.

If the brain walls are completely exposed by removing the overlying tissues, we may count the number of neural segments with complete satisfaction. In the brain of shark embryos there are fourteen pairs of segments and an anterior unsegmented tip that may represent a single pair or several consolidated pairs. This is a larger number of neural segments than has heretofore been counted for vertebrate animals. It approaches more nearly the number of head myotomes as determined by Dohrn and Killian.

Finally, we are to conclude from a study of the neural segments that the vertebrate brain is primitively segmented to its anterior tip; that its segments do not, at first, differ from those of the trunk, — in other words, they are homodynamous with those of the spinal cord, — and that there are in sharks fourteen pairs of segments.

Whitman has shown by a masterly analysis of the brain and nervous system of clepsine that the entire nervous system of annelids may be regarded as a series of brains, and that, normally, a pair of these nerve-centers, or brains, belongs to each segment. This, taken in connection with the facts set forth in this lecture, enables us to look upon the human brain, not as a homogeneous mass of tissue, but as a *complex*, composed of an aggregation of about fourteen invertebrate brains, all united into a working whole. We are to understand that its complexity has been brought about through ages of responses to external and internal influences, and its perfection of physiological action has been gradually attained. It is the highest product of evolution, the goal towards which, in the morphological world, nature has been working for countless æons of time.

NINTH LECTURE.

THE SEGMENTATION OF THE HEAD.[1]

PROF. J. S. KINGSLEY.

(TUFTS COLLEGE.)

ONE of the perennial questions is, "How many segments are there in the vertebrate head?" We have long realized that the body of a vertebrate is made up of segments as clearly marked as those of a grasshopper or crayfish. Is the head similarly constituted?

The first one to suggest such a condition was that mystical naturalist, Oken. As he tells the story, he was walking in the Harz Forest in 1806, when he found the blanched skull of a sheep. His remark upon picking it up was, "It is a vertebral column." The next year, when appointed professor extraordinary at Jena, he took for his inaugural address the subject, "The significance of the cranial bones," in which he maintained that the skull was composed of three vertebræ, — the eye, jaw, and ear or tongue vertebræ of his nomenclature. Human skulls separated into these three vertebræ may be had in the shops to-day, and looking at one of them we are struck with the genius of Oken's idea.

Thirteen years later Göthe claimed the discovery as his own, but time has settled the claim in Oken's favor.

Oken's theory maintained at least a tacit acceptance for many years, and reached its highest expression in the work of Owen. Oken's followers tried to carry it further and to include other structures than the skull. Thus in the trunk-

[1] The complete paper, of which this is a short abstract, will be published elsewhere at an early date, with full references to the literature, etc.

region the nerves find their exit between the vertebræ, and so they should do in the cranial region, the number of such segmental nerves being of course one less than the number of vertebræ recognized in the head. So those who followed Oken arranged all the cranial nerves in two groups, while those who thought they saw an additional or nose vertebra, collected the nerves in three divisions. Here must be enumerated the labors of Stieda, Johannes Müller, Stannius, and others.

Stannius, however, took another set of structures, the gill clefts, into consideration, and although he admitted only three groups of these nerves (since he recognized four vertebræ) he still says that "the number of the branches of each cranial nerve, and the number of spinal-like (segmental) cranial nerves is determined not so much by the number of cranial nerves as by that of the visceral arches."

To Gegenbaur is usually given the credit of building upon this foundation, but we must not forget that in 1869 Huxley claimed that no part of the skull was vertebral in its nature, and that not only skeletal, but all structures should be invoked in settling the question. It would not do to make the bones the basis, and work everything else to fit. So, dismissing the bones, Huxley took cranial nerves and gill clefts as his basis. Behind the ear, the nerves split above each cleft, and send a nerve to each of its margins. Here the relationships are clear, and the segments can readily be distinguished. In front of the ear, however, there is more difficulty. The facial nerve splits in the same way, above what is known in sharks as the spiracle, a cleft which persists in man as the Eustachian tube. For the next nerve in front, there is at first sight no cleft, but Huxley advanced the suggestion, often attributed to Dohrn, that the mouth had been formed by the coalescence of a pair of gill slits, and upon this supposition, this nerve, the trigeminal, was partly brought into harmony. But not all of it; there are branches which go farther forward, and for a cleft for these the orbito-nasal fissure of the embryo was suggested. Still another cleft still farther in front was advocated, so that Huxley recognized in the head nine segments,— four in front of the ear, and five behind.

Two years later (1871) Gegenbaur attacked the same problem, and between his results and those of Huxley there is much similarity. With him the cranial nerves are the primary test, and he tries to bring the gill clefts into accordance with them.

Of the cranial nerves modern human anatomists recognize twelve pairs, known by name and number as follows:—

I.	Olfactory.	VII.	Facial.
II.	Optic.	VIII.	Auditory.
III.	Oculomotor	IX.	Glossopharyngeal.
IV.	Trochlearis.	X.	Vagus (Pneumogastric).
V.	Trigeminal.	XI.	Spinal Accessory.
VI.	Abducens.	XII.	Hypoglossal.

Like Huxley, Gegenbaur at once threw three of these out of discussion, for it was thought that the nerves of special sense—olfactory, optic, auditory—differed from the rest in their mode of growth,—were, in fact, outgrowths of the brain proper. Others, from the nature of their functions, were relegated to a secondary position. As long ago as 1807, Sir Charles Bell had pointed out that the nerves of the spinal cord had two roots, the dorsal one with an enlargement, or ganglion, the ventral non-ganglionated, and that these roots differed entirely in their function. Through the dorsal root, sensations were brought from the peripheral parts to the brain, while through the ventral root the actions of the muscles and other structures were controlled. Hence, since his time, these roots have been called respectively sensory and motor. In the brain-region, however, this distinction of roots is not so clearly shown. Some of the nerves, like the third, fourth, and sixth, have purely motor functions, and these motor nerves were consequently relegated to a secondary position; dorsal or sensory roots were taken as a test.

Now, applying these ideas, Gegenbaur concluded that since the vagus nerve was distributed to several gill clefts, it must be regarded as a composite nerve, while the glossopharyngeal, supplying a single cleft, was simple, as also was the facial. The trigeminal, however, had too many branches to supply a single cleft, and so this was regarded as a double nerve.

Another feature needs mention. The gill clefts are kept from collapse by the presence of skeletal strengthening bars in the tissue between them, and these are known as the visceral or branchial arches. But there were not enough of these to correspond with all the nerves, so Gegenbaur called in small cartilages found in the lips of certain sharks, which he regarded as remnants of such arches. His whole results are summarized by him in a table :—

Primary Visceral Skeleton.	Modified Visceral Skeleton.	Nerve.	
1st Arch	1st upper Labial Cartilage	Ramus, 2	Trigemini
2d Arch	2d upper and 1st lower Labial Cartilages	Ramus, 3	
3d Arch	Mandibular Arch	Facial	
4th Arch	Hyoid Arch	Glossopharyngeal	
5th Arch	1st Gill Arch	Ramus branch, 1	Vagi
6th Arch	2d Gill Arch	Ramus branch, 2	
7th Arch	3d Gill Arch	Ramus branch, 3	
8th Arch	4th Gill Arch	Ramus branch, 4	
9th Arch	5th Gill Arch		

Gegenbaur did something more ; he gave the vertebrate theory its final quietus, for he pointed out that in the lowest fishes, where one would naturally expect, were Oken's view true, that the vertebræ of the skull would be most typical, the cranium was actually a solid case without the slightest trace of segmentation. Further, in the higher groups, cranial "vertebræ" can scarcely be spoken of, since the parts of which they are composed are largely of dermal origin.

Balfour was the next to introduce a new feature into the discussion. As is well known, the body cavity or cœlom becomes divided dorsally with a series of paired pouches which were formerly thought to give rise to the vertebræ, and hence were called protovertebræ. They are now known to produce the muscles of the trunk, and are called myotomes. In the trunk-region these are the most markedly segmental of any structures, and appear very early. Balfour pointed out that the primitive body cavity extended into the head, and that this portion also becomes divided in much the same way as that of the trunk. So with him "head-cavities" are the test of cephalic segmentation. As there is much similarity between his results and those of his pupil Marshall, we may omit a discussion of Balfour's conclusions and give those of Marshall in more detail, merely saying that Balfour recognized only eight segments in the head, with possibly one more.

Marshall uses both head-cavities and nerves in determining the segments, and he tried to bring gill slits into harmony with these. He examined those nerves admittedly segmental, and formulated the characteristics which a segmental nerve must have. The results to which this brought him may be seen from the table, but some explanations may be pardoned.

<table>
<tr><th>Segment.</th><th>Nerve.</th><th>Visceral Cleft.</th><th>Visceral Arch.</th></tr>
<tr><td rowspan="2">1 Preoral</td><td rowspan="2">I Olfactory</td><td rowspan="2">Olfactory</td><td rowspan="3"></td></tr>
<tr></tr>
<tr><td rowspan="2">2 Preoral</td><td rowspan="2">III Oculomotor
IV Trochlearis</td><td rowspan="2">Lachrymal</td></tr>
<tr><td rowspan="2">Maxillary</td></tr>
<tr><td rowspan="2">3 Oral</td><td rowspan="2">V Trigeminal</td><td rowspan="2">Buccal</td></tr>
<tr><td rowspan="2">Mandibular</td></tr>
<tr><td rowspan="2">4 Postoral</td><td rowspan="2">VII Facial
VI Abducens.</td><td rowspan="2">Spiracular</td></tr>
<tr><td rowspan="2">Hyoid</td></tr>
<tr><td rowspan="2">5 Postoral</td><td rowspan="2">IX Glossopharyngeal</td><td rowspan="2">1st Branchial</td></tr>
<tr><td rowspan="2">1st Branchial</td></tr>
<tr><td rowspan="2">6 Postoral</td><td rowspan="2">X Vagus, 1st branch</td><td rowspan="2">2d Branchial</td></tr>
<tr><td rowspan="2">2d Branchial</td></tr>
<tr><td rowspan="2">7 Postoral</td><td rowspan="2">X Vagus, 2d branch</td><td rowspan="2">3d Branchial</td></tr>
<tr><td rowspan="2">3d Branchial</td></tr>
<tr><td rowspan="2">8 Postoral</td><td rowspan="2">X Vagus, 3d branch</td><td rowspan="2">4th Branchial</td></tr>
<tr><td rowspan="2">4th Branchial</td></tr>
<tr><td rowspan="2">9 Postoral</td><td rowspan="2">X Vagus, 4th branch</td><td rowspan="2">5th Branchial</td></tr>
<tr><td rowspan="2">5th Branchial</td></tr>
<tr><td rowspan="2">10 Postoral</td><td rowspan="2">X Vagus, 5th branch</td><td rowspan="2">6th Branchial</td></tr>
<tr><td rowspan="2">6th Branchial</td></tr>
<tr><td rowspan="2">11 Postoral</td><td rowspan="2">X Vagus, 6th branch</td><td rowspan="2">7th Branchial</td></tr>
<tr><td></td></tr>
</table>

First, the olfactory nerve was brought into the category of the segmental nerves, for Marshall points out that in its development it resembles the other nerves, and is not a prolongation of the brain substance, that it possesses a ganglion, and finally it splits distally to embrace the olfactory organ, just as the facial or glossopharyngeal splits to pass on either side of the corresponding visceral cleft. From this relationship he is led to regard the olfactory organ as a gill cleft, comparing the folds of the Schneiderian membrane with the gills themselves, regardless of the fact that the one is ectodermal, the other entodermal in origin. Second, the fact that the trochlearis arises from the dorsal crest of the brain, and that the oculomotor was thought to be primarily connected with the ciliary ganglion, leads Marshall to assign these motor nerves segmental value. The increase in segments behind is due to the fact that Marshall regarded sharks like Heptanchus, with seven gill slits, as the more primitive. Regarding the rest of the table nothing need now be said, but we must point out, thirdly, that the history of some of the head-cavities was traced. They were found to be connected at first, and their separation into distinct bodies was shown to be independent of the formation of gill slits. The history of two of these cavities was followed, and these two were found to give rise to some of the muscles which move the eyeball.

At almost the same time that Marshall published his last paper, Van Wijhe gave to the world the results of his studies, and his paper is one of the most frequently quoted in connection with the subject. Head-cavities form the basis of his work, and of these he finds nine in the shark. Since his numbering of these has been almost universally followed, we may enumerate them with some detail, giving their fates as determined by Van Wijhe. The first pair of cavities are premandibular in position, and in the later development give rise to the muscles rectus superior, inferior, internus, and inferior oblique, all of which are controlled by the oculomotor nerve. The second cavity is above the mandibular arch, and sends a branch into it. This cavity gives rise to the superior oblique eye muscle, and is innervated by the trochlearis nerve. The third cavity lies above the hyoid arch, and is finally converted into the external rectus muscle, controlled by the abducens nerve. The fourth cavity, also, lies partly in the hyoid arch. The rest follow in regular sequence, interrupted only by the auditory organ. Of these latter the fourth and fifth degenerate, the sixth produces a few small muscle fibers, while the rest unite in forming the ventral prolongation of the sternohyoid muscle. From these facts Van Wijhe concludes that there are nine segments in the head, and that the hyoid arch is really double.

The nerves are carefully studied in connection with these somites. The olfactory and optic nerves are omitted from the discussion, since, among other points, they are in front of the segments. It is interesting to note that Van Wijhe shows that the optic nerve is really the most anterior of all the cranial nerves. With the remaining nerves the attempt is made to distinguish dorsal and ventral roots. The results can be seen in this condensed copy of Van Wijhe's table: —

Somite.	Muscles from the Somite.	Ventral Nerve Root.	Dorsal Nerve Root.
1	Rect. sup., inf., int., and inf. oblique	Oculomotor	Ophthalmicus profundus
2	Superior oblique	Trochlearis	Trigeminus less Ophth. prof.
3	Rectus externus	Abducens	Acusticofacialis (3–4)
4	none	none	
5	none	none	Glossopharyngeal
6	very rudimentary	not recognizable	Vagus (6–9)
7, 8, 9	Muscles from skull to shoulder girdle, with anterior part of sterno-hyoid	Hypoglossus	

Since Van Wijhe's time numerous attempts have been made to add to his structure, and in most of these the nerves have been made especial objects of study, and the results would be of great interest had we opportunity for their discussion. Most of these deal with the components of the several nerves, with the true relationships of the ciliary ganglion, with the position to be accorded the eleventh nerve, and with the question whether there be primitively a dorsal root to the hypoglossal. The head-cavities, too, are discussed. On the one hand, Rabl, in a most valuable summary of our knowledge of the whole subject, cannot find all of Van Wijhe's cavities, while Dohrn does not regard the eye muscles as comparable to the muscles of the trunk, — a conclusion to which he is led, among other reasons, by his view that the lens of the eye is a modified branchial cleft. On the other hand, there are others who find more head-cavities than Van Wijhe, and among these is to be enumerated Miss Platt, who has found one undoubted cavity in front of the most anterior one of the Dutch anatomist. Dohrn and Killian go much further, and find eighteen or nineteen of these structures, but their work can be dismissed with few words. It is, in fact, difficult to say what Dohrn's opinions are. He is most fertile in hypotheses, and he never takes the trouble to bring his later views into any harmony with the old ones. At one time every thickening of ectoderm or entoderm is a gill cleft, again every hole in the mesoderm is a head-cavity, in the third view the abducens is a complex of at least six nerves. But we are getting ahead of our story.

To Froriep and Beard we owe the introduction of a new element into the discussion, that termed by Beard "branchial sense-organs." These authors independently discovered that certain of the cranial nerves fuse with the ectoderm a short distance from the brain. From this fusion two structures are developed: one the ganglion of the nerve, from which the fibers of the permanent nerve grow back into the brain; the other, the more superficial portion, forms the Anlage of a sense-organ situated in the branchial region just above a gill cleft. These sense-organs are regarded by Beard as segmental in nature, and hence, if we count these sense-organs, we at the same time count the metameres of the head. So, proceeding on this basis, Beard finds eleven segments in the head, and arranges the nerves to fit in the way which can readily be seen from the diagram. Among the interesting features is the recognition of the olfactory as a segmental nerve; though the nasal organ is not regarded as a branchial cleft, but as a sense-organ (cf. Marshall). The facial is also regarded as a compound nerve, and the auditory nerve is segmental because it supplies the ear, which, like the nose, is in the same category of segmental sense-organs.

Segment.	Dorsal Nerve Root.	Branchial Cleft.	Nature of Sense-Organ of Cleft.	Ganglion.	Head-Cavity.	Ventral Nerve Root.
I	Olfactory	none	Olfactory Organ	Olfactory	none	none
II	Radix longa of Ciliary Ganglion.	none, or Hypophysis	Branchial	Ciliary	first	Oculo-motor
III	Trigeminus	Mouth	Branchial	Gasserian	second	Trochlear
IV	Facial	absent	Branchial	Facial	third	Abducens
V		Branchial	Branchial		?	none
VI	Auditory	none	Auditory Organ	Auditory	none	none
VII	Glosso-pharyngeal	1st Branchial	Branchial	Glosso-pharyngeal	?	none
VIII	Vagus I	2d Branchial	Branchial	Vagus I	none	none
IX	Vagus II, III, and IV	3d, 4th, and 5th Branchial	Branchial	Vagus II, III, and IV	none	none
X			Branchial			
XI			Branchial			

In the year preceding Beard's paper Ahlborn maintained that there were two distinct kinds of segmentation in the head,—the one of the mesoderm, mesomery, the other of the alimentary canal, branchiomery,—and that these two were independent and not causally related. His views have had not a little influence on subsequent work, but it must be said that it is not a difficult matter to answer his arguments, and indeed to show that, so far as our present knowledge goes, branchiomery and mesomery are in good accord.

Within the last few years another test of segmentation has been adduced, that of the segments (neuromeres or encephalomeres) of the brain. These structures had been noticed by several of the older writers upon the development of the nervous system, but little weight was given them until Kupffer brought them prominently into notice as possibly affording another clue to the segmentation of the head. The idea was further carried out by Beranek, Orr, Waters, McClure, Zimmermann, and others, and may be stated in its present form somewhat as follows. Besides the division of the brain into its several regions, — fore-brain, 'twixt-brain, etc., — this structure shows in its earlier stages another segmentation, most plainly seen in its lateral walls. For instance, the medullary region is seen to consist laterally of a series of paired enlargements, separated by vertical constrictions, and of these back to the vagus there are six (Orr) or seven (Hoffmann). These neuromeres bear a definite relation to the nerves, one pair of these arising from each neuromere, except that between the acusticofacialis and glossopharyngeal.[1] In the other brain-regions there are four more of these enlargements, two in the primitive fore-brain and two in the mid-brain, — a total of eleven back to and including the vagus.

Hoffmann has made a most important discovery in connection with the development of the cranial nerves. He finds that the segmental head nerves and the dorsal roots of the spinal nerve arise not from a solid neural crest, but are paired segmental out-pocketings (*Ausstulpungen*) of the dorsal part of the nervous cord itself. For the details of the matter reference must be made to Hoffmann's paper, but we may point out that a most important inference is to be drawn from this account. Briefly, then, the segmental cranial nerves (trigeminal, glossopharyngeal, etc.) arise as hollow outgrowths from the wall of the cerebral tube; these outgrowths reach the skin of the sides of the head, fuse with it, and from the thickening thus produced the ganglion of the nerve is formed. From this ganglion the permanent nerve grows back to the brain, the primary nerve disappearing.

[1] Hoffmann finds an Anlage of a nerve here at an early stage. It later aborts, and cannot be regarded as forming a part of the auditory nerve.

Exactly the same conditions occur in the formation of the optic nerve. It arises as a hollow outgrowth from the dorsal[1] part of the wall of the brain, which reaches the ectoderm, if it does not actually fuse with it. From the distal portion of this outgrowth is formed the ganglionic layer of the retina, corresponding exactly to the Anlage of the gasserian ganglion, and from this ganglionic layer the observations of Keibel, Froriep, and Assheton have shown that the permanent optic nerve grows back to the brain, the primitive optic stalk becoming aborted. So that, then, there appears no escape from the view that the optic nerve, instead of being a structure *sui generis*, is clearly homologous with the other admittedly segmental cranial nerves, — trigeminal, glossopharyngeal, etc. The same discovery also opens up other possibilities; besides offering a possible explanation of the mooted question of the origin of the vertebrate eye, it renders it necessary to take into account in considering the neural segmentation of the head the little understood pinealis and the secondary epiphysial structures, for, as Locy has shown, there are two paired outgrowths from the brain walls behind, and apparently serially homologous with the optic outgrowths, and these become developed into what we may collectively term the epiphysial structures. It is hence possible that we are to look in this region for some of the long-sought dorsal roots.

Lastly to be mentioned is the earlier segmentation of the neural structures discovered by Locy. He points out that in the very early stages of the embryos of elasmobranchs, batrachians, and the chick, before the medullary plate has begun to close, its margins are ornamented with a series of bead-like prominences, and that the series of these are continued back into the trunk-region, and in elasmobranchs they can even be traced into the embryonic rim (affording some puzzling problems to those who deny concrescence in the formation of the vertebrate embryo). In the expanded head-plate of the dog-fish he finds eleven of these beads on either side, and, following the history of these through until other landmarks come into view,

[1] Morphologically dorsal; the later hypertrophy of the posterior part of the dorsal surface forces it to an apparently ventral position.

concludes that the eleventh of these coincides with the position of the future vagus. The fate of these beads is followed with some detail, and is regarded as of paramount importance in settling the vexed question of the metamerism of the head.

It may be that further observations will show that Locy is right, but more evidence is greatly to be desired. That the structures in question really exist is beyond doubt ; that they have the significance which he ascribes to them is far more problematical. In the opinions of others who have studied them the structures are less regular and less symmetrical than described, and their number is not constant. Besides, there are several discrepancies in Locy's figures, which, without explanation, seem to invalidate his conclusions. At present it seems too early to extend the term neuromeres to include these structures.

It is now nearly ninety years since the question of the segmentation of the head was first broached. Can we say to-day how many segments compose this complicated structure? Several times it has seemed that the answer was close at hand, but as frequently has the investigation of other features thrown doubts upon the previous results; and to-day, while we can say that there are certainly more than the three or four of Oken and his followers, we cannot say exactly what the number is. Before the answer is placed beyond a doubt, a number of other questions must be solved, not the least of which is the broader problem of the origin of metamerism and the relation of this condition in the vertebrates to that in the lower forms.

TENTH LECTURE.

BIBLIOGRAPHY, — A STUDY OF RESOURCES.

CHARLES SEDGWICK MINOT.

THE growth of science depends on three things : —

First. The unknown, which is discoverable.

Second. Raw knowledge.

Third. Assimilated knowledge.

Our laboratory has for its special purpose to work in the first of these fields, and every one of you ought to gain largely from the discipline and inspiration here placed at your command. Bibliography inventories the resources of the second and third field, while text-books are intended to give comprehensive surveys of the third. Now text-books are not excessively numerous, and it is not really difficult in this age of incessant advertisement to keep tally of the best text-books, their successive editions, and new rivals in one's special field of biology. Far different is the case when one wishes to retain command of the literature of original research, where the gains of raw knowledge, as I have called it above, are made. It needs but little experience to teach even the beginning student that it is excessively difficult to keep track of the numerous publications in which the current work, even in a narrow field of biology, is recorded. With these difficulties you are all more or less familiar, and know from your own experience that they are due chiefly to two factors : *first*, the very great number of the publications; *second*, their being scattered without law or order in many different publications issued in many different languages. The biological bibliographer is like an explorer in a forest, — he finds no open way to travel, but must laboriously hunt for the specimens which belong in the same class according to our intellectual systems, and which he must discover as they lie scattered, unclassified, and, all too often, concealed. In passing, let me add that one reason for the increase in number of biological articles is the change in the publication habits of the present as compared with those of a generation ago. Formerly the preparation of long and thorough monographs was the goal of ambitious investigators, but now it is the fashion to publish instead a succession of short papers. How new this tendency is you will appreciate easily by remembering that we have now a goodly number of journals devoted exclusively to very short papers, such as the *Zoologischer Anzeiger, Botanisches Centralblatt, Bibliographie Anatomique,* and many more, all of which date back only a very few years. They represent a class of scientific serials which twenty-five years ago was almost, if not quite, unknown.

It will be the main purpose of this lecture to point out the resources we have for finding the literature of a given biological theme. Before beginning this task let us consider briefly what a biological author may do to facilitate making a satisfactory bibliographical record of an article of his own. We may leave apart the literary and scientific qualities of the article, not because we fail to assign them their due prime importance, but only because we are looking at the matter from the narrower point of view of the bibliographer. Now, from this standpoint there are five points which seem to me to deserve special attention.

1. *The title,* which should be as brief as possible and nevertheless indicate the contents. I recently noted an article entitled *A Reply after Two Years.* Under what head will you enter it? When you read it you will discover that it deals with the embryology of turtles. Such a title is unpardonable, for it will cause quite unnecessary trouble to hundreds, perhaps thousands of people. It is quite as bad as the bugbear title of the medical bibliographer, *A Rare Case.* There are thousands of articles on that subject, but what is it? asks the despairing recorder. For brevity of title it is surely unnecessary to plead. Every one who has had to cite authorities

knows the vexation of having to copy a long-winded title. What a blessing it would be could we have a Linnæan system for the nomenclature of biological memoirs as well as of natural species!

2. *The table of contents.* The use of tables of contents for single articles of forty to one hundred or more pages is a recent and excellent innovation. It gives a detailed summary of the arrangement of topics, which is often of the greatest convenience. If you examine the ten volumes of our own *Journal of Morphology*, you will find many articles with tables of contents prefixed. Thus, in volume ten there are eleven articles, five of which — those by Lillie, Strong, Fish, Eycleshymer, and Morgan — have tables of contents, and of the remaining six, only one exceeds thirty pages in length. In European articles you will find the custom less frequently followed. I think that you will encounter other indications that bibliographical usages are more advanced in America than abroad. May we not attribute this difference in part to the examples set by our numerous public libraries?

3. *Reprints* should always preserve the paging of the original publication, otherwise they cannot be used for consultation or reference without needless difficulty. Publishers are wofully behindhand in this matter, and usually change the paging in reprints, sometimes even in the face of the author's protest, as I have myself recently experienced. If the paging is changed, how can we refer to any special page until we have put aside the reprint and gone to the original publication, the page number of which alone has the right to be cited?

4. *References to other authorities* need careful arrangement. If they are few, it does very well to place them at the bottom of the page. If they are numerous, the best place for them is at the end of the article, in alphabetical order by authors. For reference numbers for the single articles, there are two chief systems in vogue. One system, the older of the two, simply numbers the articles consecutively, so that when the article is completed the manuscript must be revised and the proper numbers inserted in the text. Theoretically the system is very simple and convenient, but you will soon learn that in

practice authors are apt to blunder and insert wrong numbers in the text. One set of references has to be used while writing, and when all is done another set substituted, and during the substitution mistakes are not infrequent. The other system was introduced by Professor E. L. Mark, and has met with increasing favor. In this system each article is identified by the name of the author, the date of publication, and an arbitrary catalogue sign, which last may be a single letter or digit. For example: —

MARK, E. L. 81.1. Maturation, Fecundation, and Segmentation of Limax campestris, Binney. *Bull.* Mus. Comp. Zoöl., VI, 171–625, Pls. I–V.

indicates all that is necessary. The figures 81.1 stand for the year 1881, the digits indicating the century being omitted for all years of the present century; and the single digit after the period indicates the arbitrary order of entry, — in this case that the article in question is the first one to be recorded for that author and year. Should a second article published by Professor Mark in 1881 appear in the list, it would be 81.2; but were it in 1882, it would be 82.1. Professor Mark uses a slightly different notation, letters serving for entry signs; thus the paper just cited would be recorded

MARK, E. L., '81^{a},

or,

81^{a}. MARK, E. L.

The apostrophe indicates that the two digits are omitted, but now that this system has been widely used, the apostrophe may be safely left off. If one uses Mark's system, the references may be all put in as the manuscript is written, and the articles will then group themselves. Every worker should have a card-catalogue of the publications in his own field, and to such a catalogue Mark's system is peculiarly adapted; and if it is used, it is easy to enter all references in one's manuscript, giving each paper its notation from the catalogue. While preparing my *Human Embryology* I utilized this plan for the several thousand references made in the course of the work, and can assure you that in practice the plan is very convenient and time-saving. Some of the best investigators prefer other methods of citing authorities. I can only recommend the two methods just indicated as best in my own judgment, and add that it is more important to have a *good* method than to have any special method.

5. Spare your readers *long abstracts* of previous papers. Omit most of the abstracts you are tempted to insert, and make those you do give as brief as possible. Abstracts at best are inadequate repetitions, and save in exceptional instances should be avoided, especially since there has developed such an elaborate machinery for the publication of abstracts of all important and many unimportant papers. Too often an abstract is tacked on not for any useful purpose, but only to prove that the author has read the original. On the other hand, a comprehensive review of the results collated from a number of publications may often be valuable, while separate abstracts of the same papers would be almost valueless.

About the arrangement of one's own library let me interpolate a few observations. Of course if a library is small, by which I mean of less than 500 volumes and pamphlets, no special arrangement is needed, beyond what may be the outcome of one's personal convenience. And, on the other hand, if your library be very large, you must adopt a thorough library system. Most working naturalists have, however, libraries of moderate size, the orderly and convenient arrangement of which is often a perplexing problem. The perplexity arises chiefly from the accumulation of pamphlets, which are a very valuable part of a worker's scientific library, being for the most part reprints of articles in his own special field. Now, there are three prevalent ways of treating pamphlets.

1. Bind them in volumes by authors.
2. Bind them in volumes by subjects.
3. Arrange them in boxes.

Of these three methods the last is the simplest, most expeditious, and for a library *without a catalogue* the most convenient. The boxes readily serve for a classification either by authors or subjects, as you may prefer. Of boxes for this purpose I recommend either the cheap pamphlet cases of Manilla paper, sold by stationers everywhere, or else the more convenient wooden box devised by Dr. Bowditch, and which has the advantage that when it is opened the titles of the pamphlets face you.

[Since this lecture was delivered I have used another form of pamphlet box, which seems preferable to those mentioned. It is a box made of whitewood, covered with marbled paper; it measures $4 \times 11 \times 7\frac{1}{4}$ inches; it has a common drawer-handle on the back, and is open at the front.[1] Such boxes are placed on shelves, like volumes; they present a neat appearance, and are easily pulled out or replaced. It would be desirable to have a card-holder on the back to indicate the contents upon cards, which can be changed as convenient.]

Every professional biologist ought to have a card-catalogue, serving the double purpose of a bibliography and a catalogue of his library. I can probably lay my suggestions before you most rapidly by describing my own system, which, with your permission, I will now do. This system has worked satisfactorily, but I can by no means claim for it that it is, like Pangloss' world, the best of all possible systems. The library is arranged in several groups, and the pamphlets in each group are arranged alphabetically by authors, and under each author by Mark's chronological system. First the pamphlets are separated into two primary divisions, those which are not catalogued and those which are catalogued. Those pamphlets which do not immediately concern my own lines of study are not catalogued, but are simply classified in Bowditch boxes by subjects. Thus I have a box for biographical notices, for pathology, botany, systematic entomology, microscopical methods, etc., and hundreds of pamphlets are kept readily accessible. The remaining pamphlets are all catalogued on cards of the larger standard library size, made of cardboard, not paper. Were I to start over again, I should unhesitatingly use the smaller card, 12.5×5.0 cm. (about 5×2 inches), of stiff paper.

[1] Pamphlet boxes as described, but *without handles*, may be obtained of the Library Bureau in Boston. In fastening on the handle, fairly *large* screws should be used, which may be cut off so as not to project inside and tear the pamphlets.

The plan on which the cards are written is indicated by the following form:—

WHITMAN, CHARLES O. M. 1893.1

The Inadequacy of the Cell-Theory of Development.

! Journ. Morph., VIII, 639–658.

The upper right-hand corner contains the catalogue number (Mark's system), the M showing that the pamphlet is in my collection, and that the card is not merely a bibliographical one. It is better to have the catalogue number on the left, for it is then less likely to be covered by the hand in turning over the cards. The Roman numerals are used to designate the volume, the Arabic the pages. When there are plates, the numbers of those are given also. The exclamation point at the left indicates that the card has been verified by comparison with the original publication. All my catalogued pamphlets are divided into three sets: (1) octavo unbound pamphlets; (2) octavo bound pamphlets; (3) quarto pamphlets, whether bound or unbound. When a pamphlet is bound, the card is marked "Bd." In each of the three sets the pamphlets are arranged by authors, and those of each author chronologically. Thicker pamphlets are bound singly, thinner pamphlets several together,—but binding many papers in one volume is systematically avoided. The binding costs from twelve to eighteen cents; the backs are plain black cloth, with a white paper label, on which the author's name and the catalogue numbers of the pamphlets are written by hand; the sides are covered with marbled paper. The unbound octavo pamphlets are kept in Manilla paper pamphlet-boxes. From time to time I look them through to select those which I wish to have bound.

The system described is simple, and to me it has seemed convenient and altogether satisfactory, so that I am ready to recommend it, though of course some other system may be equally good for private use.

My catalogue serves me also as a bibliography, and I maintain a list of titles, which are copied from my cards and grouped under subjects. In this way I compiled my *Bibliog-*

raphy of Vertebrate Embryology, which was published by the Boston Society of Natural History in 1893. It contains 3555 titles, and it may interest you to know that I have collected since its publication upwards of a thousand titles to be added to it. As this work is intended to result in publication, the results are written out on sheets of paper, each sheet for one subject only; were it not for publication, I should use cards for the subject catalogue also.

Let us pass to our main topic, a discussion of the means of looking up the literature of a given subject in the domain of animal morphology or physiology; in regard to other divisions of the wide territory of biology I am not competent to advise you. We will pass in review: (I) the standard bibliographies; (II) incidental bibliographies, given in connection with special memoirs, etc.; (III) current bibliographies, which we can divide into two groups: (*A*) those appearing annually, and (*B*) those appearing periodically at intervals of less than a year.

I. *Standard Bibliographies.* — The purpose and character of these is so evident that it is only necessary to enumerate them. They are: —

1. W. Engelmann. *Bibliotheca historico-naturalis.* 1 vol. 8vo. Leipzig, 1846. Covers the literature of 1700–1846.

2. Carus und Engelmann. *Bibliotheca zoologica.* 2 vols. 8vo. 1861. Covers the years of 1846–1860.

3. Taschenberg. *Bibliotheca zoologica II.* Twelve parts, with pages 1–3888, have been issued, the mammals not being yet reached. It is the continuation of Carus and Engelmann.

4. Hagen. *Bibliotheca entomologica.* Die Literatur über das ganze Gebiet der Entomologie bis zum Jahre 1862. 2 vols. 8vo. 1862.

5. Minot. *Bibliography of Vertebrate Embryology.* 4to. Boston Society of Natural History. 1893.

Important help in finding a paper, when the author is known, is given by the *Catalogue of Scientific Papers*, issued by the Royal Society of London, in spite of the enormous number of its omissions. This catalogue comprises, in all, three series of large quarto volumes. The first series, in six volumes, deals with the literature of 1800–1863; the second series, in two volumes, with the literature of 1864–1873; the third, and still unfinished series, with the literature of 1874–1883. It arranges the papers by authors, numbering those of each author consecutively through the three series. There is no classification by subjects, and no subject index, so that one can obtain a reference only in case the author is correctly known. On the score of convenience it is to be regretted that the Royal Society did not imitate the compact American model of library catalogue, but on the contrary adopted a type and arrangement which has rendered their volumes needlessly bulky and inconvenient.

Three other works, though not strictly bibliographical in the sense of those above mentioned, deserve to be named here. These are:—

1. Nomenclator zoologicus continens nomina systematica generum animalium tam viventium quam fossilium, auctore L. Agassiz. Soloduri, 1842–1846. 2d edition, 1848.

2. Nomenclator zoologicus, etc. A comite Augusto de Marschall.

3. Nomenclator zoologicus, by Samuel H. Scudder.

Agassiz's work contained (2d edition) 32,964 entries, Marschall's 19,966, Scudder's about 80,000. Mr. Scudder's work, like everything done by the distinguished president of the Marine Biological Laboratory, is a monument of painstaking industry and well-directed thoroughness, and it should be at hand for every zoölogist to consult who has a new genus to name, so that needless duplication may be avoided. Scudder's *Nomenclator* was published as Bulletin No. 19 of the United States National Museum. It was based on Agassiz's *Nomenclator*, together with the manuscript addenda, which Professor Agassiz had accumulated during a long course of years. It covers the names introduced down to the close of the year 1879. For later names consult the *Zoölogical Record*.

Finally, we are indebted to Mr. Scudder for still another work, which you will often find invaluable, namely, his *Cata-*

logue of Scientific Serials of all Countries, including the Transactions of Learned Societies in the Natural, Physical, and Mathematical Sciences, 1633–1876, published by the Library of Harvard University in 1879.

II. *Incidental Bibliographies,* or lists of authorities given in special works. As you know, every important article gives more or less extensive references to the previous literature, and one does not need long experience to appreciate the immense advantage of this custom. Especially to the great monographs do we turn for such references, and I may direct your attention especially to the splendid series known as the *Fauna and Flora of the Gulf of Naples,* which is in our library. The more important text-books usually give carefully selected lists of the more important papers. You will find such in McMurrich's *Invertebrate Morphology,* Wiedersheim's or Gegenbaur's *Comparative Anatomy,* Hertwig's *Embryology,* Korschelt and Heider's *Embryology of Invertebrates,* and other similar hand-books. But among all works of this class there stand two which are preëminently valuable for their helpfulness in guiding us to morphological and zoölogical literature; one is Milne-Edwards' *Physiologie,* in fourteen volumes (G. Masson, Paris, 1857–1881). This great work is a rich treasury of references, especially to the older literature, which it is somewhat the fashion to overlook, although it often contains things which have been forgotten, and which you would do well to make the acquaintance of, if only to learn that the broad foundations of our science were all laid before any of us were born. Milne-Edwards was thoroughly versed in the zoölogical literature of his time, with, however, a curiously abrupt limit at about 1858. In fact, though his work contains a very large number of references to papers later than 1858, the proportion of omissions is strikingly larger than for papers issued before that date. You will find the consultation of these early authorities especially valuable for anatomical information concerning all classes of animals. The present generation is so devoted to comparative morphology and general principles that real anatomical knowledge of animals has become almost a rarity. Thus I find young men who can discuss glibly the problem of the morphological (segmental) value of the trigeminal nerve, and yet cannot give exact information concerning its anatomical disposition in any animal.

Henri Milne-Edwards was born in 1800, and died in 1885. He was a typical naturalist, trained under the influence of the great Cuvier, and as a naturalist looked upon animals very differently from the modern morphologist, with whose ways he was as little able to sympathize as with the views of Darwin. In many respects the naturalist had a broader conception of zoölogy than now prevails, for to him the earth was a whole, in which rocks, animals, and plants all had their parts and mutual relations, and the comprehension of these relations was the ideal for the attainment of which he strove. You will find in Milne-Edwards' writings typical illustrations of the scientific attitude of zoölogists before the Darwinian theory was put forth, and from these illustrations one preserves an impression of loss which has befallen us through our surrendering too fully to the biological tendencies and fashions of our day. It is therefore doubly profitable to consult Milne-Edwards' *Physiologie*, for it not only collates much information not elsewhere well united, but also presents it from a point of view novel to most of us, although it was the point of view of those great men who created not only zoölogy in the narrower sense, but also physiology, comparative anatomy, and palæontology.

The other, Bronn's *Thierreich*, is doubtless well known to you all. It is a work on a vast plan, aiming, as it does, to present a comprehensive summary of our knowledge of the morphology, including also the classification, distribution, and biology of all classes of the animal kingdom. The volumes are issued in thin parts, each volume dealing with a single class. It thus happens that many years have elapsed between the beginning and the completion of a volume, — the extreme being the volume on crustacea, which was begun in 1866 and, although it has acquired great bulk, is still unfinished, though its author, Professor Gerstaecker, of Greisswald, had at the time of his death nearly terminated the work. The status of Bronn's *Thierreich* at the present time is as follows : —

Protozoa, first edition, by Bronn, completed 1859.
Protozoa, second edition, by Bütschli, completed 1889.
Sponges, by Vosmaer, completed 1887.
Actinozoa (cœlenterates and echinoderms), by Bronn, completed 1860.
Cœlenterates, second edition, by Chun (pts. 1–10).
Echinoderms, second edition, by Ludwig (pts. 1–19).
Malacozoa, by Bronn and Keferstein, completed 1866.
Mollusca, second edition, by Simroth (pts. 1–20).
Tunicates, second edition, by Seeliger (pts. 1–3).
Worms, by Pagenstecher and Braun (pts. 1–37).
Crustacea, by Gerstaecker, first half, completed 1879.
Crustacea, by Gerstaecker, second half (pts. 1–46).
Fishes, by Hubrecht (pts. 1–4).
Amphibia, by Hoffmann, completed 1878.
Reptiles, by Hoffmann, completed 1890.
Birds, by Gadow (pts. 1–49).
Mammals, by Giebel and Leche (pts. 1–41).

In all these volumes the literature is abundantly cited, and they usually include exceedingly valuable bibliographies, in most cases classified by subjects. When we consider the value of these lists of authorities, and in our minds add the value of Bronn's *Thierreich* as the fullest existing repository of zoölogical facts, we necessarily rank this invaluable compendium among the few books indispensable to every zoölogical laboratory.

III. *Current Bibliographies*, or periodicals devoted wholly or in great part to recording the current literature in a given field. We may consider such bibliographies conveniently under two heads: *first*, annual publications; *second*, periodical, that is, issued at shorter intervals.

A. *Annual Publications.* — The succession of these may be said to have been fathered by Müller's *Archiv für Anatomie, Physiologie und wissenschaftliche Medizin.* Müller's *Journal* was the continuation of Reil's, Reil and Autenrieth's, and J. F. Meckel's *Archiv.* It was begun in 1834, and is continued to-day, but in 1877 was divided into two *Abtheilungen* (*Anatomische* and *Physiologische*), each making an annual volume. The whole series constitutes the most important morphological and physiological single publication in the world. Johannes

Müller remained the editor from 1833 to 1858. He was one of the greatest scientific men Germany has produced, and ranks as pioneer and founder of three sciences: of comparative anatomy and embryology,—or, as we now prefer to say, morphology,—of experimental physiology, and of scientific pathology. He was endowed with that genius for observation and induction which alone enables a man to become a great leader in natural science. In the first volume of his *Archiv* he gives a "Jahresbericht ueber die Fortschritte der Anatomischen-physiologischen Wissenschaften im Jahre 1833." Since that time, Germany has supplied us our most important annual records or summaries. The *Jahresberichte* of Johannes Müller are most interesting reading, even to-day; they are remarkable for the clearness with which the important points are brought to notice. In later years he engaged various collaborators in this work, among whom we find Siebold, Keferstein, Reichert, and others. With Müller's death, in 1858, these reports closed.

Their place was taken by two series of Reports, one issued in connection with the *Archiv für Naturgeschichte*, the other in connection with the *Zeitschrift für Rationelle Medizin.* The former journal was founded in 1835 by Professor Wiegmann, of Berlin, and originally published with each *Heft* a report of progress in some field of zoölogy or botany; with its second year it began the system followed up to the present time, of issuing two volumes a year, the second made up entirely of reports for various branches of biology. Of late years the *Archiv für Naturgeschichte* has shown a predominant entomological tendency, both in its original articles and reports, although it still continues to cover a wide range, except that botany has entirely dropped out. Its reports are often very late in appearing, and are irregularly issued; thus the part published in November, 1894, gives the reports on entomology for 1893, on carcinology for 1891, 1892, and 1893. In spite of all these peculiarities you will find these *Berichte* often valuable.

The *Zeitschrift für Rationelle Medizin* was a first-class scientific serial. It entered upon its third series in 1857, and then began issuing, as an annual volume, a "*besondere Abtheilung*," the first of which bears this title: "*Bericht über die Fortschritte* *der Anatomie und Physiologie im Jahre 1856. Herausgegeben von Dr. J. Henle, Professor in Göttingen, und Dr. G. Meissner, Professor in Basel.*" We have here a consolidation of interests, for these *Berichte*, by Henle and Meissner, had already appeared several years independently. They continued in connection with the *Zeitschrift* until 1872 (literature of 1871). I have been informed that the cessation of the publication was due to lack of sufficient financial support. They were, however, immediately replaced by a new series of *Jahresberichte*, edited by Hoffmann and Schwalbe, later by Hermann, of Königsberg, and Schwalbe. This new series continued for twenty years, and it, like its predecessor, ceased, but unfortunately has no successor, except for the physiological part. But these *Jahresberichte* are, to a certain extent, replaced on the morphological side by the *Ergebnisse der Anatomie und Entwickelungsgeschichte*, edited by Fr. Merkel and R. Bonnet, which constitute the *Zweite Abtheilung* of the *Anatomische Hefte*. Of the "*Ergebnisse*" three volumes (1891–93) have appeared. These volumes give comprehensive summaries of groups of articles. The physiological part of the *Jahresberichte* has been continued in a very condensed form by Professor Hermann in his newly inaugurated series.

With the progress of years the annual reports have gradually changed in character. The early ones were narrative in form and critical in character. Thus, in the first report by Johannes Müller, he relates the discussions between the soberminded, and perhaps dogmatic Cuvier, and the brilliant but erratic Geoffroy Ste-Hilaire, to whom we habitually refer erroneously as Ste-Hilaire; and Müller indicates his estimate of both these eminent naturalists, and finds occasion from time to time to interpolate opinions, and even observations of his own. But gradually the personality of the reporter is withdrawn, until it has become the admitted requirement that all analyses should be impersonal abstracts. In the *Jahresberichte* of the present this requirement is entirely fulfilled, with only very rare exceptions.

There are also two series of special *Jahresberichte*, which the active worker in biology and zoölogy will find indispensable in connection with certain lines of work. The first of these is edited by Professor Baumgarten, formerly of Königsberg, at present of Tübingen. This annual bears the somewhat lengthy title, *Jahresbericht über die Fortschritte in der Lehre von den pathogenen Mikroorganismen, umfassend Bacterien, Pilze und Protozoen.* The first volume covered the literature for 1885, and the ninth volume (for 1893) is now in course of publication. The second of these is the *Jahresbericht über die Fortschritte der Thierchemie,* edited by Prof. Richard Maly, of which the first volume, published in 1873, at Vienna, covers the literature for 1871. The series is still continued, but the volumes make their appearance considerably belated.

Finally, I ought to allude — I cannot do more than that — to the botanical *Jahresbericht,* the first of whose bulky volumes was issued in 1873 by Professor Just. In appearance and arrangement of the contents this series has been closely imitated by the younger zoölogical *Jahresbericht* (begun in 1879).

We now come to the two great zoölogical records. Those which have been mentioned above are (with the exception of the *Botanischer Jahresbericht* and the reports in the *Archiv für Naturgeschichte*) all prepared in the interest of medical men, and treat their various subjects mainly, if not exclusively, from the medical standpoint. The two publications now to be mentioned are, on the contrary, adapted primarily to the needs of zoölogists. I refer, of course, to the *Zoölogical Record* and to the *Zoologischer Jahresbericht,* issued by the Zoölogical Station at Naples.

The *Zoölogical Record* was founded by Dr. Albert C. L. G. Günther, who states in the preface to the first volume, covering the literature of 1864, that "the object of the *Record* is to give in an annual volume reports on, abstracts of, and an index to the various zoölogical publications which have appeared in the preceding year ; to acquaint zoölogists with the progress of every branch of their science in all parts of the globe ; and to form a repertory which will retain its value for the student of future years." The *Zoölogical Record* has to a certain extent attained its objects, and is, indeed, an invaluable aid in finding the literature of any subject. It has suffered in reputation very much, owing to its incompleteness, its omissions being very numerous, and too often both surprising and inexcusable. You have only to compare the volumes from Naples with those of the *Record* for the corresponding years to satisfy yourselves that the criticism made is perfectly just. When, therefore, you consult the *Record*, you will usually find that there are other perhaps important articles on your subject besides those cited in the *Record*. The English standard of bibliography appears to me not to be very high either in regard to practical details of arrangement, or in regard to thoroughness. I remember that when Mr. Scudder prepared his list of scientific serials he found a large number which were entirely overlooked by the Royal Society in their great catalogue. In 1870 a special association was formed, which many naturalists joined, for the object of continuing the *Record*. In 1887 the publication was assumed by the Zoölogical Society. The yearly *Record* is sometimes more or less incomplete; thus in the volume for 1894 the reports on Crustacea, Arachnida, Myriapods, and Vermes are lacking. Incredible as it seems in such a work, there is no index of authors, but only an index of new genera! In fact, the *Record* has its chief value as an assistance to the systematic zoölogist.

The *Zoologischer Jahresbericht*, published by the Zoölogical Station at Naples, is a very thorough and admirable work. Its first seven volumes (1879–1885) covered the whole field of zoölogy, but since then it has omitted all systematic work, leaving that for the *Record*. Its matter is well arranged, and so indexed and printed that it is easy to find what one seeks. In brief, it is indispensable for every zoölogical laboratory in which anything higher than elementary work is attempted.

B. *Periodical Bibliographies.* — Under this head we have to pass in review a series of journals appearing at short intervals. These journals form two natural classes: *first*, those specially devoted to bibliography, all of which publish short original articles; *second*, those which are chiefly devoted to short abstracts of articles published elsewhere.

First Class (mainly bibliographical). — 1. *Zoologischer Anzeiger.* This valuable publication is probably well known to you all. It was founded in 1878 by the veteran zoölogist, Victor Carus, and publishes at frequent intervals lists of articles grouped according to the class to which they refer. This plan secures relatively prompt publication of the titles, but has the disadvantage that consultation of the completed volumes is exceedingly laborious, for one has to look through lists scattered irregularly through the pages. Owing to the enormous growth of zoölogical literature it was found necessary to divide the *Anzeiger* into a volume for original articles and another exclusively for bibliography.

2. *Anatomischer Anzeiger.* This journal resembles the *Zoologischer Anzeiger* very closely in plan and appearance, but differs somewhat in its scope, for it confines itself to the literature which interests the student of vertebrate morphology, and classifies the titles according to the organs to which the papers refer. This magazine was founded in 1886 by Karl Bardeleben, of Jena, and is now the official organ of the German Anatomical Society, whose proceedings are issued as an *Ergänzungsheft* of the *Anzeiger.*

3. *Bibliographie anatomique.* A journal of the same general character as the last, but its bibliographical lists are confined exclusively to articles published not in France but in French, — a restriction which necessarily appears somewhat absurd as well as characteristically provincial to us. The journal, nevertheless, is an excellent one, and contains valuable original articles, and a certain number of abstracts, which are usually good. It is edited by Professor Nicolas, of Nancy, and was started in 1893.

4. *Monitore zoologico.* This little magazine is one which ought to be more widely known in America, and deserves general support. It set the model for the French publication last mentioned, for it was started several years earlier, having begun in 1890. It gives original articles, abstracts, and lists of papers on zoölogical and morphological subjects, published by Italians, whether in the Italian language or not. Now there is a great deal of important investigation accomplished

in Italy, but owing to entire lack of first-class scientific journals in Italian, the results of these investigations are issued in all sorts of ways, — often in little-known medical journals or in the transactions of obscure scientific societies, with which Italy swarms, — and they would remain permanently unknown were it not for the painstaking records of Professor Chiarugi in his *Monitore*.

The four serials just mentioned ought to be accessible to every student and to form part of the library of every zoölogical or morphological laboratory. The remaining serials to be enumerated are certainly less essential, but for certain special purposes are almost indispensably consulted. They form my

SECOND CLASS (journals primarily devoted to publishing abstracts of papers). — I have noted the following : —

1. *Medizinisches Centralblatt*, founded in 1863, by L. Hermann.

2. *Biologisches Centralblatt*, founded in 1881, by J. Rosenthal.

3. *Gynaekologisches Centralblatt*, founded in 1877, by Dr. H. Fehling, of Stuttgart, and Dr. H. Fritsch, of Halle.

4. *Neurologisches Centralblatt*, founded in 1882, by E. Mendell.

5. *Physiologisches Centralblatt*, founded in 1887, by S. Exner and J. Gad.

6. *Zoologisches Centralblatt*, founded in 1894, by A. Schuberg.

7. *Fortschritte der Medizin*, founded in 1883, by C. Friedländer.

8. *Journal of the Royal Microscopical Society of London* gives numerous good abstracts of articles interesting to microscopists, was begun in 1878, is now issued in bi-monthly parts, forming a bulky annual volume.

9. *Virchow-Hirsch Jahresberichte*, founded in 1866 as the continuation of an earlier medical *Jahresbericht* published at Erlangen.

10. *Schmidt's Jahrbücher*, which was founded in 1834 and has grown into a series of nearly two hundred and fifty volumes. These *Jahrbücher* are literally indispensable for looking up certain lines of research through the past, as, for example, the determination of sex, the phenomena of puberty, menstruation, growth, anatomy, and physiology of infancy, senile metamorphoses, heredity, etc. On all these subjects

Schmidt's Jahrbücher will guide you to many articles of biological interest, which you are little likely to discover otherwise.

It often happens that one cannot obtain a certain original paper when needed, and in such cases an abstract of the paper wanted may be found in one or several of the ten serials just enumerated. You will notice that many of them are medical journals, and yet they are sometimes indispensable to the zoölogists and morphologists. For example, articles on the uterus and placenta, on growth, heredity, origin of sex, and many other subjects are often to be discovered through medical publications, and through medical publications only.

You have doubtless all been struck with the fact that nearly all the titles I have quoted are in German or in Latin by German authors, and have already reached the conclusion that the work of the world in recording biological literature is mainly the work of Germans. This conclusion is correct, and it is a pleasure to make a public acknowledgement of our indebtedness. Hereafter, we hope that a systematic and thorough record of zoölogical and anatomical literature will be kept by the International Bureau organized at Zürich through the efficient energy of our countryman Mr. H. H. Field. We should each look upon it as a personal obligation to support the work of this Bureau, both by coöperating with it and by subscribing to its publications.

To conclude: how is one to proceed if one wishes to find the literature of a given zoölogical or morphological subject? I should answer: consult first the principal text-books at your command, which will give you probably some of the chief authorities, by turning to which you will obtain other references; and from the papers thus traced yet other references will be secured. Unless one is dealing with some minor or detailed question, or some novel or unusual topic, one can usually obtain acquaintance with a considerable body of investigations with comparative rapidity. Next, one must consult the standard bibliographies (p. 156), and also both the various *Jahresberichte* and the current bibliographies (especially of the *Zoologischer* and of the *Anatomischer Anzeiger*). Third, consult Milne-Edwards' *Physiologie* and Bronn's *Thierreich;* or, if you can find any important monograph which certainly or probably deals with your subject, consult that, of course. Finally, if your question is one medical men are likely to have discussed, look through the Reports of Virchow-Hirsch and *Schmidt's Jahrbücher*, and also through the various medical journals of the *Centralblatt* type (see p. 166, above).

I have dealt with a difficult and, I fear, very dry subject, and can only hope that some of my suggestions will prove helpful. It is profitable to consider sometimes the ways and means of science as well as her results, for the investigator's success depends upon his mastery over both means and results, and this double mastery can be had only by those who also command the complex bibliographical resources of biology. I hope that our review of these resources will encourage some of you to enter, others to advance along the paths of research; and I trust that you all, when you leave the laboratory, will carry with you a deeper and loftier enthusiasm for original research, which is at once the chief duty and the chief privilege of the biologist.

Revised at Boston, December, 1895.

ELEVENTH LECTURE.

THE TRANSFORMATION OF SPOROPHYLLARY TO VEGETATIVE ORGANS.[1]

PROF. GEORGE F. ATKINSON.

(Cornell University, Ithaca, N.Y.)

The general effect of nutrition in plants is evident in their growth and fruiting ; but the more subtle influences, under a great variety of changing or special conditions, are but imperfectly understood. In general, an increase in food supply within the plant, external conditions being favorable, increases the entire plant product. In poor soil plants may be fed with profit, the product increasing, though not in the same ratio, with the increased supply of food. Not only is the vegetative part of the plant increased, but the fruit also, within certain limits. The ratio of increase, however, between the vegetative portion of the plant and its fruit is not constant, but changes with the varying food supply. After a given point the vegetative portion increases more rapidly than the fruit. Another striking influence of increased food supply is that a point is reached soon where the fruit portion decreases, or is even completely suppressed, while the vegetative portion still increases. Our knowledge of these disproportionate and antagonistic relationships between the vegetative and reproductive portions of the plant is largely empirical, though some of it is based on direct experimentation. It is not surprising, therefore, that even among botanists there should be differences of opinion concerning the fundamental laws governing these relationships.

The genus Onoclea, as well as some others, presents an interesting dimorphism of the leaves, some of the leaves being

[1] See Plates I–VIII at close of volume.

devoted exclusively to the vegetative function, while others are devoted exclusively to the reproductive function. In Onoclea the vegetative leaf forms a large expanded triangular lamina, which is divided into several large pinnæ with rudimentary lobes or pinnules. The reproductive leaves, or sporophylls, are built on much the same general plan, but are much shorter, with the pinnæ and pinnules also much shorter and narrower, and the edges inrolled, entirely concealing the sporangia, as if they were enclosed in carpellary structures, though the sporophyll has not become a closed structure, such as is found in the ovary of higher plants. The inrolled pinnæ are closely appressed against the rachis of the sporophyll.

Besides this structural dimorphism of the leaves they present what is sometimes termed a seasonal dimorphism, — *i.e.* the vegetative leaves are the first to appear in the season, from April and May until July, while the sporophylls appear in July, or the latter part of June. During the first part of the season the vegetative or nutritive system of the plant is built up, while during the latter part of the season the reproductive function is in the ascendant. Occasionally an abnormal state of the leaf in *Onoclea sensibilis* is found, in which both functions are united in a single leaf, a portion of the leaf being expanded and resembling the vegetative leaf, while some of the pinnæ are more or less rudimentary, revolute, and sporiferous, representing an intermediate stage between the truly vegetative leaf and the typical sporophyll. This form of the leaf was once described as a variety — *obtusilobata* Torrey — of this species of Onoclea, though later it was regarded as "a rare abnormal state in which the pinnæ of some of the sterile fronds, becoming again pinnatifid, and more or less contracted, bear some fruit dots without being much revolute or losing their foliaceous character."[1] The language here suggests that the sterile leaf becomes partly transformed into a fertile leaf, in accordance with the old ideas of metamorphosis. More recently,[2] from the discovery of a number of the forms of this

[1] Gray's Manual, 5th ed., p. 668. The same form of the plant was known as the species *O. obtusilobata* Schkuhr, *idem*.

[2] Underwood: Bull. Torr. Bot. Club, Vol. VIII; *Bot. Gaz.*, 1881, p. 101.

species in a meadow, it was suggested that this state resulted from some injury to the sterile leaf, so that the vegetative function was forced upon the very young sporophylls, causing them to expand more or less, while the sporangia and sori were correspondingly decreased. This suggestion met with considerable opposition. Later the suggestion was adopted and published by another, and upon this the following criticism appeared in *Nature*, April 15, 1894: "The remark quoted . . . about the probable cause of the cases where the fronds of Onoclea have an intermediate character between the usual sterile and fertile conditions, is one of those sage observations which it is easy to make, but which observed facts hardly or not at all sustain."

Although an experiment had been planned for the purpose of attempting to induce this form artificially by cutting off the early vegetative leaves, this criticism really "set the machinery in motion," for without experimental proof such an empirical proposition lacked an essential foundation for argument. The locality selected for carrying on the experiment was in the vicinity of Ithaca, N.Y., on the flats not far from the head of Cayuga Lake. The first cutting of the leaves was made May 11, when they were twelve to eighteen inches high. It was feared at the time that the experiment had been postponed too long to obtain the desired results, as it seemed within the bounds of possibility that already the vegetative function might have been carried on for a sufficient time for the manufacture of what carbohydrates the plant would need for the perfect development of the reproductive portion. The intention was then to cut the leaves about once each week, in order that the plants could derive very little benefit from the later developed sterile leaves. Heavy rains, however, prevented access to the localities until June 9, when the leaves were cut a second time. The second leaves had reached approximately the same size as the first crop, and still by this time there was no sign of the development of the fertile leaves, either in the experiment plat or in adjacent plants which had been left as checks.

July 12 a third visit was made to the locality on the Ithaca flats, where the larger number of ferns were. Diligent search at this time revealed nothing which at first could be understood to be the fertile leaf in the experiment plat, and the knife was used for the third time. While cutting the third crop of leaves occasionally one was seen which appeared quite different from the ordinary sterile leaves. The pinnules were fully expanded, and the lobes appeared nearly normal in form, but the venation was somewhat more prominent, and this gave the appearance which first attracted attention. After critical examination there were seen peculiar and very small whitish flakes or scales on the under surface of the pinnules. These, with the aid of a pocket lens, were readily seen to be partially aborted indusia, located either directly across or at the side of the veinlets. The pleasure at the discovery of this result was considerably dampened by the thought that the experiment might prove to have been too radical by cutting the leaves more than once. Further examination revealed what appeared to be still younger fertile leaves which would not be so fully expanded when grown. At this date there were observed in the adjacent undisturbed plants several normal sporophylls partially developed. July 29 another examination was made, and quite a number of leaves were found which would be taken for quite typical cases of the form of the species.

August 8 and 9, all the plants showing these results were gathered and photographed, a portion of the stem, or rhizome, was taken with each plant in order to show some, at least, of the bases of the leaves which had been amputated, as well as the recently developed sterile leaves for comparison. Nearly thirty such plants were gathered, and more than twenty of these were photographed, in order to preserve an accurate record of the many variations which presented themselves.

In the normal sporophyll, the pinnæ are quite closely approximated on one side of the rachis. The fertile pinnules are closely revolute, and the margins very much shortened, so that each pinnule forms a small, oval, pocket-shaped or slipper-shaped sack, open only at a point near the attachment with the mid-vein of the pinna. These pinnules possess two to four pairs of lateral veinlets. Upon these lateral veinlets are the placentæ, seated rather near the base, and the true indusium is situated across the base of the veinlet, near, or a little distant from, the mid-vein, and arches slightly outward, or away from the mid-vein, partially covering the group of sporangia.

The first step in the transformation of the sporophyll is the lateral spreading of the pinnæ, so that they stand out more or less strongly in a plane corresponding to that of the vegetative leaf. At the same time there occurs a partial unfolding of the revolute pinnule. This occurs by an increase in the number of cells of the lamina, and a corresponding decrease in the growth of the cells which go to form the sori. The marginal cells of the lamina increase more rapidly than those toward the mid-vein and the base. A few of the terminal pinnæ in the normal sporophyll bear no pinnules, but are very much like the pinnules of the lower pinnæ. The simplest condition of the unfolding of the revolute pinnæ or pinnules is the partial expansion of these terminal ones, more advanced stages proceeding along down from the terminal portions of the pinnules.

The grades of transition are correlated with the circinate development of the leaf, the later developed portions showing a more highly developed vegetative expansion and function than the early developed portions of the same leaf. The pinnæ then, in the simplest and intermediate stages, have a more or less clavate or spathulate outline. The pinnules in an individual pinna may vary from quite strongly revolute ones to those which are fully expanded and nearly plane.

Occasionally transformed fertile leaves are found which show a tendency to an abortive development, *i.e.* they remain quite small, the stipe rather short, the pinnæ and pinnules very short, though they may be quite fully expanded.

Comparing individual sporophylls, all grades of transition are present from the completely differentiated fertile leaf to the sterile one. In several cases it was impossible to determine with certainty to which phase of the dimorphism the leaf primarily belonged, or for which it was originally intended. Some of these leaves which were at first doubtful were finally found to possess rudimentary indusia on a few of the lower pinnæ, these occurring on the basal pinnules.

The fully or partially expanded pinnules, when the transformation has not been carried too far, are more or less obtuse.

The venation also is very prominent, and strong in contrast with that of the sterile leaf, especially the lateral veinlets of the pinnules. This character is quite persistent, and enables one to differentiate the leaves frequently when no indusia are present, and the pinnules are not obtuse, or no more so than those of the normal sterile leaves.

One transformed sporophyll had a length of twenty-five cm., and a spread of pinnæ twenty-two cm. in extent. A very few of the basal pinnules had their margins slightly revolute, and quite a number of indusia were present, while very few of the pinnules were obtuse. The venation of the entire leaf was quite coarse and very prominent.

During the expansion of the pinnules, the position of the indusia changes somewhat, and its form, to a very great extent. It becomes located at a greater distance from the base of the lateral veinlets, the distance depending to some extent upon the extent of the transformation of the pinnule. In broadly expanded pinnules at the termination of the pinnæ, the indusia are frequently moved on to veinlets of the second and third order, instead of those of the first order.

While indusia are present on partially or nearly expanded pinnules, or frequently on fully expanded ones, sporangia appear to occur only on those which are entirely normal, or only partially expanded. Passing through the various transitions of the pinnules, from the normal fertile ones to those which are little more than half expanded, the sporangia vary, gradually decreasing in number and perfection of development, as the pinnules partake more and more of the vegetative character. In the partially expanded pinnules, the indusium is frequently so small that it affords very little protection to the sporangia, and the location of rudimentary sporangia is often at a considerable distance from the indusium.

When the leaf has lost so much of its reproductive function that the sporangia are becoming rare or rudimentary in the sorus, apospory frequently occurs, and the placenta develops among the rudimentary sporangia prothalloid growths. These are filamentous, lanceolate, or spathulate in form, the two latter forms being two or more cells wide. The cells are richly provided with chlorophyll, but thus far no antheridia or archegonia have been found. These prothalloid growths resemble very much some of those which are developed from the placental region of *Pteris aquilina* L., and first described by Doctor Farlow in the *Annals of Botany*, II, 1888, p. 383. The same condition of *Pteris aquilina* was noted by myself in the autumn of 1893, at Ithaca, N. Y.

When the experiment with *Onoclea sensibilis* was undertaken, no serious thought was given to an attempt to produce like conditions by artificial treatment with the other species of this genus, namely, *Onoclea struthiopteris*. However, on July 14, after observing the result which was attending the experiment with *Onoclea sensibilis*, I determined to try the *Onoclea struthiopteris* even at this late date. The fern is very abundant on an island in Fall Creek, where vegetation is very rank and the leaves of the ostrich fern attain a height of 150 cm. or more. The leaves from fifty or sixty stools of this fern were cut away, the leaves then having attained their maximum height for this locality. In this number of stools there were half a dozen in which there were fertile leaves already 15–25 cm. in height.

The experiment was inspected on August 10. The fertile leaves which were up on the 14th of July had matured their sporangia and were, to all appearance, normal. There were many rudimentary fertile leaves only partly unrolled, three to six inches in height. These were also found among the stools of the fern which had not been disturbed. For a long time during the spring, the ground here was under water, and this may have had some influence in aborting many of these leaves. That many of them were of the fertile kind was manifest by the peculiar revolute character of the rudimentary pinnules.

Very few of the stools from which the leaves had been cut on the 14th of July had put forth new leaves. Ten or twelve had produced one to four leaves, ranging from one to two feet high. Very careful search was made to discover some sign of a sporophyll partially transformed, and I was about to conclude that the experiment was a failure for that year because entered upon at so late a date. At last a single leaf was found in a stool where were three freshly developed sterile leaves. The sterile leaves were 60–75 cm. in height, and the transformed sporophyll about 30 cm. The leaf was somewhat injured by accident, perhaps by the knife when cutting the sterile leaves on the 14th. The pinnæ were fully expanded, yet markedly different from those of the sterile leaves, being only toothed, while the pinnæ of the sterile leaves are deeply cut and possess quite acute pinnules. The teeth, or pinnules, of the transformed fertile leaf were obtuse or rounded. This was the only marked difference at first observed, and I did not feel warranted in concluding that it was a fertile leaf until examination with a pocket lens revealed plainly a number of rudimentary indusia. There were no sporangia, however, not even rudimentary ones, and none of the pinnules were at all revolute.

The experiment with *Onoclea struthiopteris* being somewhat unsatisfactory, because undertaken so late in the season, was renewed this year (1895). The first vegetative leaves were cut early in May, when they were about 40 or 50 cm. long. This species differs markedly from *Onoclea sensibilis* in the vernation of the leaves. Those of *Onoclea sensibilis* are developed successively one by one on a prostrate rhizome, or stem, which advances so rapidly that the leaves of one season stand in a row. In *Onoclea struthiopteris* the stem is perpendicular and increases in length very slowly, the leaves being developed in rosettes, a half dozen, more or less, at one time.

The experiment plat was visited a second time early in June, and a second rosette of leaves had developed from the stools which had been cut in May. This time the leaves were about 30 cm. high. None of the sporophylls had appeared, and the leaves were cut again. Leaves from undisturbed plants were also cut at this date. Late in June a few of the sporophylls were appearing from a very few of the untreated plants, but none as yet showed from the amputated plants, though another large rosette of vegetative leaves had developed. The season was a very dry one, and very few sporophylls had developed, and for this reason the experiment was considered a failure. However, July 29th a sudden impulse seized me to visit the experiment plat again, and this time not in vain, for eight to ten plants had each from one to four partially transformed sporophylls. These presented a great variety of stages in the transition, though in no case had the transformed sporophylls reached the size and expansion of the vegetative leaves as in the case of *Onoclea sensibilis*. They were quite young, however, and probably later in the season would have been larger and more expanded.

These plants were nearly all removed to the laboratory at the time in order to photograph and study them. In general the transformation of the sporophylls of *Onoclea struthiopteris* agrees with that of *Onoclea sensibilis* in that the distal portion of the leaf and of the pinnæ expand more than the proximal portion, these latter parts bearing either normal sporangia and sori, or showing them in various stages of degradation and suppression. At that time no prothalloid growths could be discerned with the eye, or with the aid of a pocket lens. Perhaps they might appear later in the season, since the sporophylls were much younger than those on *Onoclea sensibilis* on which they occurred.

The results of these experiments are entirely in harmony with a law which many recognize to exist between the vegetative and reproductive functions of plants, and indeed animals as well. They serve, however, to demonstrate clearly this relation which in many cases has been observed empirically rather than demonstrated by definite tests. In these ferns, the fact that there is a complete differentiation between the sterile and fertile leaves, and that the sterile leaves develop quite far in advance of the fertile ones, makes the case peculiarly adapted to present a beautiful demonstration of the law. A certain development of the vegetative phase is necessary in order to provide for the necessary nutriment which the reproductive phase requires. If the vegetative leaves are destroyed or removed before this function is so far completed as to enable the complete development of the reproductive phase, the latter will necessarily decrease, and there will be an effort on the part of the plant to provide as quickly as possible for the furtherance of the vegetative functions. This can most quickly be attained by the partial or complete expansion of leaves which had begun to be differentiated as fertile ones, for the general plan of structure of the sterile and fertile leaves is very much the same, especially in a very early stage of their development. The different degrees of fixation of the reproductive characters on these very young fertile leaves, at the time when the plant is suddenly deprived of the fully developed vegetative leaves, determines to a great extent the individual character of the transformed structure which assumes the responsibility for the entire labor of the leaf system heretofore definitely divided between different individual leaves or structures. This individual character is also influenced to a certain extent by the readiness with which the individual plant puts forth new vegetative leaves. So with the various combinations of these two conditions there results the very wide variation which is here presented in the forms of the transformed fertile leaves, showing almost every conceivable gradation which we could naturally expect when we take into consideration the course of development of the ordinary leaves. The extremes of these variations present very doubtful cases. On the one hand, there are fertile leaves which have felt the slightest touch of this influence controlling the transformation, and it is extremely difficult to say whether it is entirely normal or not. On the other hand, there are cases where the greatest demand has been made upon a leaf of the fertile kind at so early a period in its development that it becomes to all intents and purposes a vegetative leaf, and possesses so little of the individuality of the fertile leaf that we cannot, in our ignorance, discriminate it from a leaf of the vegetative kind.

The plan this season, though not carefully originated, was to extend the experiments to phanerogamous plants in order to see, especially, if the pistils, which are supposed to be homologous sporophyllary organs, could be forced to take on the form and function of the vegetative leaves by cutting off the latter. This part of the experiment, I say, was not well originated, since, on account of numerous other duties, no selection of plants was made until operations were begun in the spring. For this reason some of the plants operated on were too far advanced, while others were ill chosen, because the sporophylls appeared at the same time as the vegetative leaves. This latter difficulty presented itself especially in the case of *Podophyllum peltatum*, *Arisæma triphyllum*, and *Aralia nudicaulis*. In *Geranium maculatum*, *Smilacina racemosa*, *Angelica atropurpurea*, and *Veratrum viride* the sporophyllary organs were too far advanced.

While direct experimental evidence seems to be lacking, there is enough of empirical evidence to show that the transformation of the sporophyllary organs to vegetative ones takes place quite frequently in certain species of the phanerogams.

Transformations of the andræcium, or stamens (microsporophylls), is not a very common occurrence, though it is recorded in the case of several species, *Petunia*, *Jatropha pohliana* Müll. (Müller, *Mem. Soc. Phys. et Hist. Nat.*, Geneva, Tome XVII), *Trifolium repens*, cultivated species of Rosa, etc. Transformations of the pistils, or gynæcium (macrosporophylls), are much more common and remarkable. In the double-flowering cherry the ovary is changed often to a small foliar organ, frequently the margins separated thus exposing the ovules, while the tip has a slender style and imperfect stigma. Moquin relates a case in a tulip where the ovary was represented by true leaves with ovules on their margins. This frequently happens in the columbine and in members of the Cruciferæ and Umbelliferæ. In Vitis sometimes the pistil is foliaceous, with the ovules on their inner surface (Planchon et Mares, *Ann. Sci. Nat.*, Ser. 5, Tome VI, p. 228, 1866). If the ovary is the homologue of the macrosporophyll in the strobilus of the Archegoniatæ, as Bower suggests, then the opening of the ovary and the exposure of the ovules, or macrosporangia, under the influence of changed or disturbed conditions of nutrition, must be looked upon as a partial reversion in *form only, not a reversion in function.* This is accompanied by a more or less complete sterilization of the sporogenous tissue, the expansion of the blade into a well-developed foliar organ, and the assumption of the vegetative function in place of the reproductive one.

The philosophy of these changes, viewed not only in the light of immediate causes, but also from the standpoint of phylogeny of the foliar organs of the sporophyte, teaches that they proceed from the sporophyllary to the vegetative organs. This study has led rather unexpectedly to questions of deeper import than were in mind at the start. It suggests more than the mere adaptation of the sporophyll to the form and function of the vegetative leaf, directed by some influence which tends at the time to force that function on it. It suggests that in general vegetative leaves may have been derived from sporophylls.

In other words, these results lend force to the proposition offered by Bower (*Ann. Bot.*, VIII, pp. 343–365, 1894) that the sporophylls are primary organs, the vegetative leaves secondary ones, and that sporophylls never have been derived from foliage shoots, but that the converse is true.

Aside from the questions of homology and phylogeny of foliage shoots and sporophylls, another one presents itself, which suggests that one of the potent influences in the evolution of vegetative organs on the sporophyte was a disturbance of the carbon assimilatory function of the gametophyte in the gradual passage of plants from an aquatic to a terrestrial life. This is a purely theoretical consideration, and probably must always remain so, though it is quite probable that artificial injury to the gametophyte could be made to result in the sterilization of sporogenous tissue, which was the first step toward the evolution of sporophytic vegetative organs. However, considering the sporophyte alone, we have seen how artificial injury can be made to influence the advance of a sporophyll to a foliage shoot within a single life cycle, — a demonstration of phylogeny in ontogeny.

PLATE I.—Onoclea Sensibilis, normal form.

Plate II. — Onoclea Sensibilis, with partially transformed sporophylls.

PLATE III. — Onoclea Sensibilis, with partially transformed sporophyll.

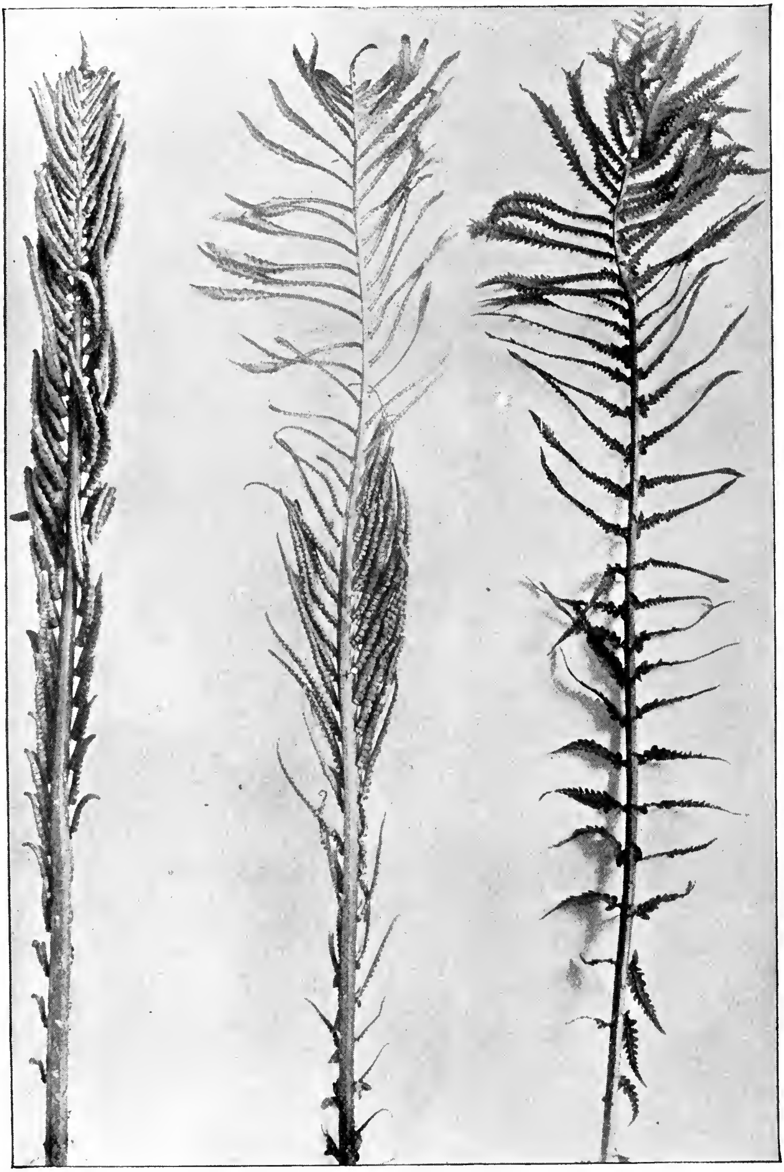
Plate IV. — Onoclea Sensibilis, with two completely transformed sporophylls.

a *b*

Plate V. — Onoclea Sensibilis. *a* normal form of sporophyll. *b* partially transformed sporophyll, showing "fruit dots."

PLATE VI. — Onoclea Sensibilis, lower portion of partially transformed sporophyll magnified.

PLATE VII. — Onoclea Struthiopteris. The four small leaves are sporophylls: one is normal, the others partially transformed.



a b c

PLATE VIII. — Onoclea Struthiopteris. *a* normal sporophyll. *b* partially transformed sporophyll. *c* completely transformed sporophyll.

128